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Advancing butterfly systematics through genomic analysis

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ABSTRACT. Within the framework of an ongoing comparative genomic study of global butterfly diversity, we construct phylogenetic trees combining all protein-coding genes assembled from the whole genome shotgun data. When viewed in the context of current taxonomy and phenotypic knowledge, the genome-wide phylogeny points to further advances in butterfly systematics, which are presented here. We assign major clades with comparable levels of genetic divergence to the same taxonomic rank and apply criteria involving relative population divergence and gene flow to define species boundaries. As a result, one genus, 13 subgenera, 62 species, and five subspecies are proposed as new (type species in original combinations or type localities are given in parentheses): a genus *Ajenorix* Grishin, **gen. n.** (*Rapala hypargyria* Elwes, 1893) in Deudorigini Doherty, 1886, Lycaenidae [Leach], [1815]; subgenera: in Riodinidae Grote, 1895 (1827): *Ouida* Grishin, **subgen. n.** (*Dodona ouida* Hewitson, 1866) and *Egeona* Grishin, **subgen. n.** (*Taxila egeon* Westwood, 1851) of *Dodona* Hewitson, 1861, *Locris* Grishin, **subgen. n.** (*Lasaia oileus* Godman, 1903) of *Lasaia* H. Bates, 1868, *Lucispila* Grishin, **subgen. n.** (*Hesperia lucianus* Fabricius, 1793) of *Parvospila* J. Hall, 2018, *Byzia* Grishin, **subgen. n.** (*Lemonias byzeres* Hewitson, 1872) of *Zelotaea* H. Bates, 1868, *Arichlosyne* Grishin, **subgen. n.** (*Apodemia ochracea* Mengel, 1902) of *Aricoris* Westwood, 1851, and *Lenca* Grishin, **subgen. n.** (*Lemonias lencates* Hewitson, 1875) of *Pachythone* H. Bates, 1868; in Lycaenidae: *Afrix* Grishin, **subgen. n.** (*Dipsas antalus* Hopffer, 1855) of *Capys* Hewitson, 1865, *Wacus* Grishin, **subgen. n.** (*Myrina epirus* C. Felder, 1860) of *Deudorix* Hewitson, 1863, and *Crates* Grishin, **subgen. n.** (*Hesperia isocrates* Fabricius, 1793) of *Virachola* F. Moore, 1881; and in Hesperiidae Latreille, 1809: *Ochloba* Grishin, **subgen. n.** (*Poanes batesi* Bell, 1935), *Ochlata* Grishin, **subgen. n.** (*Hesperia venata* Bremer & Grey, 1853), and *Ochluma* Grishin, **subgen. n.** (*Hesperia yuma* W. H. Edwards, 1873) of *Ochlodes* Scudder, 1872; species: in Riodinidae: *Lasaia cola* Grishin, **sp. n.** (Mexico: Colima), *Curvie wing* Grishin, **sp. n.** (USA: Texas), *Curvie westwing* Grishin, **sp. n.** (Mexico: Sonora), *Curvie chiapensis* Grishin, **sp. n.** (Mexico: Chiapas), *Emesis* (*Tenedia*) *tinia* Grishin, **sp. n.** (Argentina), *Emesis* (*Tenedia*) *guaya* Grishin, **sp. n.** (Uruguay), *Emesis* (*Aphacitis*) *bugaba* Grishin, **sp. n.** (Panama: Chiriquí), and *Synargis rectanga* Grishin, **sp. n.** (Peru: San Martin) and in Hesperiidae: *Phanus ecutinus* Grishin, **sp. n.** (Ecuador: Pichincha), *Entheus zeus* Grishin, **sp. n.** (Brazil: Amazonas), *Entheus guyaneus* Grishin, **sp. n.** (Guyana), *Entheus colombeus* Grishin, **sp. n.** (eastern Colombia), *Entheus proxemus* Grishin, **sp. n.** (Brazil: Pará), *Entheus peruveus* Grishin, **sp. n.** (Peru: Madre de Dios), *Entheus hyponota* Grishin, **sp. n.** (Brazil: Amazonas), *Entheus lina* Grishin, **sp. n.** (Brazil: Pará), *Entheus guato* Grishin, **sp. n.** (Mexico: Chiapas), *Entheus pano* Grishin, **sp. n.** (Panama: Darién), *Entheus venezuelius* Grishin, **sp. n.** (Venezuela: Aragua), *Entheus ecuadius* Grishin, **sp. n.** (Ecuador: Napo), *Entheus bogoteus* Grishin, **sp. n.** (Colombia: Bogotá), *Cecropterus* (*Thorybes*) *notochlorothrix* Grishin, **sp. n.** (Brazil: Santa Catarina), *Urbanus* (*Urbanoides*) *elma* Grishin, **sp. n.** (Venezuela: Merida), *Telegonus* (*Rhabdoides*) *missionus* Grishin, **sp. n.** (USA: Texas), *Telegonus* (*Rhabdoides*) *panavenus* Grishin, **sp. n.** (Panama: Panamá), *Telegonus* (*Rhabdoides*) *pacificus* Grishin, **sp. n.** (Peru: Piura), *Telegonus* (*Rhabdoides*) *amazonicus* Grishin, **sp. n.** (Brazil: Rondônia), *Telegonus* (*Rhabdoides*) *pallidus* Grishin, **sp. n.** (Panama: Darién), *Telegonus* (*Rhabdoides*) *subfuscus* Grishin, **sp. n.** (Brazil: Santa Catarina), *Telegonus* (*Rhabdoides*) *elorianus* Grishin, **sp. n.** (likely Southeast or South Brazil), *Telegonus* (*Rhabdoides*) *perumazon* Grishin, **sp. n.** (Peru: Madre de Dios), *Telegonus* (*Rhabdoides*) *steinhauseri* Grishin, **sp. n.** (Mexico: Veracruz), *Telegonus* (*Rhabdoides*) *chiapus* Grishin, **sp. n.** (Mexico: Chiapas), *Telegonus* (*Rhabdoides*) *colotrix* Grishin, **sp. n.** (Colombia: Cauca), *Telegonus* (*Rhabdoides*) *flavimargo* Grishin, **sp. n.** (Costa Rica: Limón), *Telegonus* (*Rhabdoides*) *sobrasus* Grishin, **sp. n.** (Brazil: Santa Catarina), *Telegonus* (*Rhabdoides*) *chuchuvianus* Grishin, **sp. n.** (Ecuador: Esmeraldas), *Telegonus* (*Rhabdoides*) *panamus* Grishin, **sp. n.** (Panama: Panamá Oeste), *Telegonus* (*Rhabdoides*) *tatus* Grishin, **sp. n.** (Panama: Panamá), *Telegonus* (*Rhabdoides*) *fulvimargo* Grishin, **sp. n.** (Peru: Cuzco), *Telegonus* (*Rhabdoides*) *alardinus* Grishin, **sp. n.** (Brazil: Rio de Janeiro), *Pellicia* (*Hemipteris*) *cina* Grishin, **sp. n.** (Brazil: Rondônia), *Gorgopas trochicuz* Grishin, **sp. n.** (Peru: Cuzco), *Gorgopas trocha* Grishin, **sp. n.** (Colombia: Tolima), *Gorgopas trochitango* Grishin, **sp. n.** (Argentina: Salta), *Perus* (*Perus*) *perus* Grishin, **sp.**

n. (Peru: Amazonas), *Gomalia westafra* Grishin, **sp. n.** (Ghana: Oti), *Chirgus* (*Chirgus*) *argentinus* Grishin, **sp. n.** (Argentina: Jujuy), *Chirgus* (*Chirgus*) *teres* Grishin, **sp. n.** (Peru: Junín), *Chirgus* (*Chirgus*) *sombrus* Grishin, **sp. n.** (Peru: Puno), *Zopyrion* (*Zopyrion*) *xerxes* Grishin, **sp. n.** (Honduras: San Pedro Sula), *Anisochoria bacchoides* Grishin, **sp. n.** (El Salvador: La Libertad), *Onespa nuba* Grishin, **sp. n.** (Mexico: Oaxaca), *Vacerra tama* Grishin, **sp. n.** (Mexico: Tamaulipas), *Vacerra saltina* Grishin, **sp. n.** (Argentina: Salta), *Vacerra cuza* Grishin, **sp. n.** (Peru: Cuzco), *Oligoria* (*Oligoria*) *tinalandia* Grishin, **sp. n.** (Ecuador: Santo Domingo de los Tsáchilas), *Eutychide trombella* Grishin, **sp. n.** (Costa Rica: Heredia), *Talides hispina* Grishin, **sp. n.** (Ecuador: Napo), *Damas honduras* Grishin, **sp. n.** (Honduras: San Pedro Sula), *Damas kenos* Grishin, **sp. n.** (Peru: Loreto), and *Damas lavandas* Grishin, **sp. n.** (Peru: Madre de Dios); and subspecies: in Nymphalidae Rafinesque, 1815: *Erebia* (*Erebia*) *pawloskii bilibinia* Grishin, **ssp. n.** (Russia: Chukotka) and in Hesperiidae: *Telegonus* (*Rhabdoides*) *alector ecuadoricus* Grishin, **ssp. n.** (Ecuador: Esmeraldas), *Hesperia pahaska tehaska* Grishin, **ssp. n.** (USA: Texas), *Hesperia pahaska hidalgo* Grishin, **ssp. n.** (Mexico: Hidalgo), and *Hesperia pahaska bajanorta* Grishin, **ssp. n.** (Mexico: Baja California Norte). The following are valid genera: *Uraneis* Bates, 1868, **stat. rest.** (not *Thisbe* Hübner, [1819]) and *Virachola* F. Moore, 1881, **stat. rest.** (not *Deudorix* Hewitson, 1863). The following are valid subgenera, not genera or synonyms: *Balonca* F. Moore, 1901, **stat. rest.** of *Dodona* Hewitson, 1861, *Ariconias* J. Hall & Harvey, 2002, **stat. nov.** of *Aricoris* Westwood, 1851, *Thisbe* Hübner, [1819], **stat. nov.** of *Lemonias* Hübner, [1807], and *Pseudonymphidia* Callaghan, 1985, **stat. nov.** of *Pachythone* H. Bates, 1868. The following are valid species, not subspecies or synonyms: *Erebia* (*Erebia*) *pawloskii* Ménétriés, 1859, **stat. conf.** (not *Erebia* (*Erebia*) *theano* (Tauscher, 1806) or *Erebia* (*Erebia*) *stubbendorfii* Ménétriés, 1847), *Erebia* (*Erebia*) *demmia* B. Warren, 1936, **stat. nov.** (not *Erebia* (*Erebia*) *pawloskii* Ménétriés, 1859), *Lasaia oaxacensis* Grishin, 2024, **stat. nov.** (not *Lasaia sessilis* Schaus, 1890), *Curvie yucatanensis* (Godman & Salvin, 1886), **stat. rest.** (not *Curvie emesia* (Hewitson, 1867)), *Entheus talaus* (Linnaeus, 1763), **stat. rest.** and *Entheus pralina* Evans, 1952, **stat. nov.** (not *Entheus priassus* (Linnaeus, 1758)), *Entheus dius* Mabille, 1898, **stat. rest.**, *Entheus aequatorius* Mabille & Boullet, 1919, **stat. rest.**, *Entheus latifascius* M. Hering, 1925, **stat. rest.**, and *Entheus marmato* Salazar & Vargas, [2017], **stat. nov.** (not *Entheus matho* Godman & Salvin, 1879), *Cecropterus* (*Thorybes*) *coxeyi* (Williams, 1931), **stat. rest.** (not *Cecropterus* (*Thorybes*) *egregius* (Butler, 1870)), *Cecropterus* (*Thorybes*) *chlorothrix* (Röber, 1925), **stat. rest.** (not *Cecropterus* (*Thorybes*) *virescens* (Mabille, 1877)), *Telegonus* (*Rhabdoides*) *hopfferi* (Plötz, 1881), **stat. rest.** (not *Telegonus* (*Rhabdoides*) *alector* (C. Felder & R. Felder, 1867)), *Telegonus* (*Rhabdoides*) *gilberti* (H. Freeman, 1969), **stat. rest.** (not *Telegonus* (*Rhabdoides*) *hopfferi* (Plötz, 1881), **stat. rest**), *Telegonus* (*Rhabdoides*) *bifascia* (Herrich-Schäffer, 1869), **stat. conf.** and *Telegonus* (*Rhabdoides*) *tinda* (Evans, 1952), **stat. conf.** (not *Telegonus* (*Rhabdoides*) *latimargo* (Herrich-Schäffer, 1869)), *Telegonus* (*Rhabdoides*) *parmenides* (Stoll, 1781), **stat. rest.**, *Telegonus* (*Rhabdoides*) *crana* (Evans, 1952), **stat. nov.**, and *Telegonus* (*Rhabdoides*) *cyprus* (Evans, 1952), **stat. nov.** (not *Telegonus* (*Rhabdoides*) *creteus* (Cramer, 1780)), *Telegonus* (*Rhabdoides*) *erana* (Evans, 1952), **stat. nov.** and *Telegonus* (*Rhabdoides*) *meretrix* (Hewitson, 1876), **stat. rest.** (not *Telegonus* (*Rhabdoides*) *chiriquensis* Staudinger, 1875), *Telegonus* (*Rhabdoides*) *grullus* (Mabille, 1888), **stat. rest.** (not *Telegonus* (*Rhabdoides*) *latimargo* (Herrich-Schäffer, 1869)), *Pellicia* (*Hemipteris*) *meno* (Mabille, 1889), **stat. rest.** and *Pellicia* (*Hemipteris*) *zamia* (Plötz, 1882), **stat. rest.** (not *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870), *Pellicia* (*Hemipteris*) *fumida* Mabille, 1889, **stat. rest.**, *Pellicia* (*Hemipteris*) *aequatoria* Williams & Bell, 1939, **stat. rest.**, and *Pellicia* (*Hemipteris*) *toza* Evans, 1953, **stat. nov.** (not *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882), *Pellicia* (*Hemipteris*) *naja* Steinhauser, 1989, **stat. nov.** (not *Pellicia vecina* Schaus, 1902, **syn. nov.**), *Gomalia litoralis* Swinhoe, 1885, **stat. rest.** (not *Gomalia albofasciata* F. Moore, 1879), *Chirgus* (*Chirgus*) *biseriatus* (Weymer, 1890), **stat. rest.** (not *Chirgus* (*Chirgus*) *limbata* (Erschoff, 1876)), *Chirgus* (*Chirgus*) *trisignatus* (Mabille, 1875), **stat. rest.** (not *Chirgus* (*Chirgus*) *bocchoris* (Hewitson, 1874)), *Zopyrion* (*Zopyrion*) *thyas* Evans, 1953, **stat. nov.** (not *Zopyrion* (*Zopyrion*) *subvariegata* Hayward, 1942), *Vacerra cecropterus* (Draudt, 1923), **stat. rest.** (not *Vacerra hermesia* (Hewitson, 1870)), and *Damas corope* (Herrich-Schäffer, 1869), **stat. rest.**, *Damas cervus* (Möschler, 1877), **stat. rest.**, and *Damas angulis* (Plötz, 1886), **stat. rest.** (not *Damas clavus* (Herrich-Schäffer, 1869). The following are valid subspecies, not species or synonyms: *Erebia* (*Erebia*) *pawloskii sajana* Staudinger, 1894 **stat. rest.** (not *Erebia* (*Erebia*) *pawloskii pawloskii* Ménétriés, 1859), *Pellicia* (*Pellicia*) *dimidiata brasiliensis* R. Williams & E. Bell, 1939, **stat. rest.** (not a synonym of *Pellicia* (*Hemipteris*) *meno* (Mabille, 1889), **stat. rest.**), *Chirgus* (*Chirgus*) *biseriatus barrosi* Ureta, 1956, **stat. nov.**, *Chirgus* (*Chirgus*) *bocchoris cuzcona* Draudt, 1923, **stat. conf.**, and *Damas angulis ampyx* (Mabille, 1891), **stat. nov.** (not a synonym of *Damas clavus* (Herrich-Schäffer, 1869)). *Phareas serenus* Plötz, 1883, **syn. rev.** is a junior objective synonym of *Papilio talaus* Linnaeus, 1763. The following are junior subjective synonyms, new or transferred between taxa: *Esthemopheles* Röber, 1903, **syn. rev.** of *Uraneis* Bates, 1868, **stat. rest.**, (not of *Thisbe* Hübner, [1819]), *Eudamus oenander* Hewitson, 1876, **syn. nov.** of *Aroma aroma* (Hewitson, 1867), *Aethilla weymeri* Plötz, 1882, **syn. rev.** of *Telegonus* (*Rhabdoides*) *chiriquensis* Staudinger, 1875, *Telegonus fabrici* Ehrmann, 1918, **syn. rev.** of *Telegonus* (*Rhabdoides*) *latimargo* (Herrich-Schäffer, 1869) (not *Telegonus* (*Rhabdoides*) *alardus* (Stoll, 1790), *Arteurotia demetrius* Plötz, 1882, **syn. nov.** and *Pellicia vecina* Schaus, 1902, **syn. nov.** of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882, *Carystus orope* Capronnier, 1874, **syn. rev.** of *Tigasis corope* (Herrich-Schäffer, 1869) (not of *Damas corope* (Herrich-Schäffer, 1869)), *Damas woldi* Shuey, 2024, **syn. nov.** of *Damas corope* (Herrich-Schäffer, 1869), **stat. rest.**, and *Thracides polles* Godman, 1901, **syn. rev.** and *Perichares tripuncta* Draudt, 1923, **syn. rev.** of *Damas angulis ampyx* (Mabille, 1891), **stat. nov.** (not of *Damas corope* (Herrich-Schäffer, 1869)). *Pilodeudorix batikelides* (W. Holland, 1920) (not *Deudorix* Hewitson, 1863) is a **new** genus-species **combination** and the following are new species-subspecies combinations: *Telegonus* (*Rhabdoides*) *bifascia siges* Mabille, 1903 (not *Telegonus* (*Rhabdoides*) *creteus* (Cramer, 1780)), *Telegonus* (*Rhabdoides*) *latimargo aquila* Evans, 1952 (not *Telegonus* (*Rhabdoides*) *alardus* (Stoll, 1790), and *Gomalia jeanneli levana* Benyamini, 1990, (not *Gomalia elma* (Trimen, 1862)). **Lectotypes** are designated for 24 taxa: *Phareas serenus* Plötz, 1883 (the Amazonian

region), *Peleus aeacus* Swainson, 1831 (South America), *Entheus matho* Godman & Salvin, 1879 (Nicaragua), *Eudamus hopfferi* Plötz, 1881 (Mexico, likely south-central or southern), *Telegonus bifascia* (Herrich-Schäffer, 1869) (Brazil), *Telegonus chiriquensis* Staudinger, 1875 (Panama: Chiriquí), *Aethilla weymeri* Plötz, 1882 (likely Panama: Chiriquí), *Pellicia zamia* Plötz, 1882 (likely Venezuela), *Pellicia tyana* Plötz, 1882 (Brazil: likely São Paulo), *Arteurotia demetrius* Plötz, 1882 (Brazil: likely Rio de Janeiro), *Pellicia violacea* Mabille, 1891 (Brazil: likely Rio de Janeiro), *Pellicia vecina* Schaus, 1902 (Brazil: Rio de Janeiro), *Pellicia bilinea* Mabille, 1889 (Panama: Chiriquí), *Pholisora clytius* Godman & Salvin, 1897 (Mexico: Nayarit), *Bolla semitincta* Dyar, 1924 (Mexico: Colima), *Carterocephalus biseriatus* Weymer, 1890 (Bolivia), *Zopyrion sandace* Godman & Salvin, 1896 (Mexico: Guerrero), *Goniloba clavus* Herrich-Schäffer, 1869 (Southeast and South Brazil), *Goniloba corope* Herrich-Schäffer, 1869 (the Amazonian region, likely Suriname), *Hesperia crataea* Hewitson, 1876 (Brazil: Bahia), *Proteides cervus* Möschler, 1877 (Suriname), *Proteides ampyx* Mabille, 1891 (Panama: Chiriquí), *Thracides polles* Godman, 1901 (Panama: Chiriquí), and *Carystus orope* Capronnier, 1874 (Southeast or South Brazil). **Neotypes** are designated for six taxa: *Papilio priassus* Linnaeus, 1758 (Suriname), *Papilio talaus* Linnaeus, 1763 (the Amazonian region), *Papilio peleus* Linnaeus, 1763 (French Guiana), *Peleus aeacus* Swainson, 1831 (French Guiana), *Eudamus blasius* Plötz, 1881 (Southeast or South Brazil), and *Hesperia angulis* Plötz, 1886 (Panama: Panama). The type locality of *Perichares tripuncta* Draudt, 1923 is not in South Brazil, but likely in Panama: Chiriquí, as deduced by genomic comparison. *Chlosyne flavula blackmorei* Pelham, 2008 and *Chlosyne palla sterope* (W. H. Edwards, 1870) may be sympatric in British Columbia, Canada, and *Lon co* Grishin, 2023 is sympatric with *Lon ma* Grishin, 2023 in Monteverde, Costa Rica. Additional specimens of *Cecropterus* (*Thorybes*) *viridissimus* Grishin, 2023 confirm it as a species-level taxon, and *Aethilla toxeus* Plötz, 1882 is confirmed as a junior subjective synonym of *Cecropterus* (*Murgaria*) *albociliatus albociliatus* (Mabille, 1877) by further genomic sequencing. The holotype of *Cecropterus* (*Thorybes*) *oaxacensis* Grishin, 2023 is illustrated after being spread. Curiously, *Onespa gala* (Godman, 1900) and *Onespa brockorum* Austin & A. Warren, 2009 lack overall genetic differentiation typical of species-level taxa. Furthermore, preliminary taxonomic lists of *Entheus* Hübner, [1819] and *Telegonus* (*Rhabdoides*) Scudder, 1889 (from the clade analyzed in this work) are given. Finally, unless stated otherwise, all subgenera, species, subspecies, and synonyms of mentioned genera, subgenera, and species are transferred together with their parent taxa, and taxa not mentioned in this work remain as previously classified.

Key words: taxonomy, classification, genomics, phylogeny, biodiversity.

ZooBank registration: http://zoobank.org/FFC1AD90-AA2D-4B41-8A75-383B7AD99212

INTRODUCTION AND METHODS

This study builds upon investigations initiated through the genomic sequencing of butterflies and applies similar concepts and methods as in our previous works (Cong et al. 2019a, b; Li et al. 2019; Zhang et al. 2019a–d; Cong et al. 2020; Zhang et al. 2020b; Cong et al. 2021; Zhang et al. 2021; Robbins et al. 2022; Zhang et al. 2022b, d; Zhang et al. 2023b, d, e; Zhang et al. 2024a–c; Zhang et al. 2025). The goal is to refine butterfly classification through genomic analysis. To achieve this, we examine a broad array of butterfly taxa from across the world. These specimens, which originate primarily from both museum and private collections (see Acknowledgments for specific sources), span a temporal range from newly collected to those around 250 years old. When possible, DNA is extracted from primary type specimens to ensure an objective genomic reference for species names (Cong et al. 2021; Zhang et al. 2022a). DNA extraction is usually carried out from a leg, and we follow a non-destructive protocol that maintains the integrity of the leg, which can subsequently be used in morphological studies. If the DNA is not already degraded due to specimen age, it is fragmented before genomic library preparation. Sequencing is performed using the Illumina next-generation platform, producing 150-base pair (bp) reads. Our protocol does not depend on targeted gene or fragment amplification; instead, it sequences all DNA fragments retrieved. This makes the method equally effective for older specimens with highly fragmented DNA, typically 30–50 bp.

From each specimen, we use sequencing data—specifically, fragments that are 150 bp or shorter—to reconstruct exons of protein-coding genes. These are assembled with guidance from the reference genome of a phylogenetically close relative, for which an assembled genome is available. These reconstructed genes are then used to infer phylogenetic relationships. We generate three phylogenetic trees using IQ-TREE v1.6.12 with the GTR+GAMMA model (Nguyen et al. 2015): one from autosomes (nuclear genome), one based on genes inferred to reside on the Z chromosome, and another from mitochondrial DNA. Unless specified in the figure legends, we randomly sample 100,000 codons—roughly 2% of the total codon dataset, equating to 300,000 base pairs—for constructing nuclear

phylogenies in a timely fashion. Branch support in the resulting trees is evaluated using 100 replicate samples, each comprising 10,000 randomly selected codons. Phylogenetic trees are reconstructed for each replicate, and support values (ranging from 0 to 100) correspond to the number of replicates that share the same bipartition as the main tree constructed from 100,000 codons. In many analyses, instead of this limited sampling, we incorporate more codons—typically all well-covered positions as specified in the figure legends—and employ ultrafast bootstrap support (Minh et al. 2013). Additional details on the methodology are provided in our earlier works (Li et al. 2019; Zhang et al. 2022b).

Phylogenetic trees are displayed, color-coded, and rotated using FigTree (Rambaut 2018). Existing taxonomic classification is mapped onto these trees to detect non-monophyletic taxa and identify clades corresponding to unnamed groups. Genome-based trees frequently display "levels"—points in evolutionary history where multiple lineages diversified concurrently (Zhang et al. 2021). These synchronized radiations are often associated with geological events that affected multiple butterfly lineages at the same time. Such patterns provide a framework to align taxonomic ranks (e.g., tribe, subtribe, genus, subgenus) with diversification levels apparent in genomic trees. This approach promotes a taxonomic structure that is both internally consistent and evolutionarily justified, incorporating both genetic divergence and paleontological context. The application of consistent principles is a step towards a more stable classification. Our classification decisions are primarily informed by genomic trees, with morphological traits as corroborative evidence. The rationale for this emphasis is that genomes offer a more comprehensive and informative representation of the organism than adult morphology, which has traditionally been the cornerstone of butterfly taxonomy. Genomes contain information not only on adult phenotypes but also on life history traits, habitat use, reproductive behavior, and diet. While we are not yet able to directly infer phenotypes from genomic sequences, we can utilize aggregated DNA data from protein-coding regions as a genetic proxy and a robustly inferred phylogeny as a guide for classification decisions. This supports the development of a taxonomic framework that is consistent with phylogenetic relationships and evolutionary principles.

The taxa we propose are monophyletic and align with prominent clades. By “prominent,” we mean branches within the phylogenetic tree that have high statistical support—typically showing 100% consistency across replicates—and are generally longer than adjacent branches. The length of a branch corresponds to the number of base-pair substitutions it represents. Longer branches not only tend to have stronger support values, but the accumulated genetic changes also often lead to observable differences in phenotype. These phenotypic differences may appear in morphological traits that are not always evident in adults but may exist in larval stages or various aspects of biology. However, the relationship between genetic divergence and visible phenotypic change is highly nonlinear (Zhang et al. 2019a). Therefore, some short branches may also correspond to morphologically distinct taxa. Each case must be assessed individually. It remains debatable whether a visible adult morphological difference resulting from a small number of genetic alterations—such as a single genomic inversion—warrants recognition as a separate taxon, especially if traits like larval morphology remain unchanged. Our taxonomic framework is grounded in the existing classification, using currently valid names and their associated ranks as a baseline for identifying levels within phylogenetic trees and establishing new taxa.

Although this work addresses several broader classification issues—such as redefining genera, proposing new genera and subgenera, and reassigning species to ensure monophyly—our main emphasis is at the species and subspecies levels. Species boundaries are defined using multiple lines of evidence: differentiation in the Z chromosome with F_{st} values above 0.20 (which generally indicates species-level separation), G_{min} values below 0.05 (signifying limited gene flow) (Cong et al. 2019a), differences in COI barcode sequences (typically greater than 2%) (Hebert et al. 2003) and their correlations with phenotypic differences (Lukhtanov et al. 2016), and the presence of distinct, well-supported clades in phylogenetic trees (Zhang et al. 2022d). However, mitochondrial markers like COI often introgress between species (Bachtrog et al. 2006; Cong et al. 2017a), meaning that some distinct species may show similar or identical barcodes (Burns et al. 2008; Zhang et al. 2023a). Additional details can be found in Zhang et al. (2022a), in the section “Species, subspecies, and genomics.”

Traditionally, subspecies are considered to be geographically distinct populations that exhibit consistent phenotypic differences (for example, if 70% of individuals can be identified by phenotype alone, without knowledge of location) but are capable of interbreeding (Mayr 1982; Monroe 1982). In practice, reproductive compatibility is hard to verify, and wing pattern differences alone usually define subspecies in butterflies. It is rarely clear whether these differences are genetic or environmentally induced. By analyzing genomic sequences, we can compare populations based on their genotypes. In this study, we describe new subspecies for populations that form distinct genomic clades—visible in at least one of the trees—and are genetically distinct, though not to the degree that defines species. These subspecies represent early stages of speciation—diverging populations that have not yet reached full species status. After identifying these clades, we examine their wing patterns to identify diagnostic traits in phenotypes. As is typical for subspecies, these diagnostic traits are statistical: they may be present in about 70% of individuals, with exceptions expected. However, since our subspecies are defined as genomic clades, DNA-based characters supporting these clades are more robust than phenotypic characters and apply to nearly all specimens. For this reason, we provide DNA-based diagnoses for each new subspecies described.

The main sections of this study are organized taxonomically, following a genome-scale phylogeny supplemented by morphological data. For newly proposed taxa, we include brief descriptions of diagnostic phenotypic traits—often with citations that offer identification keys and more detailed descriptions and illustrations—as well as diagnostic DNA characters from the nuclear genome and, where possible, from the COI barcode. These DNA characters come from protein-coding regions and were identified using our established protocol (see SI Appendix in Li et al. (2019)). Our character selection method, described in Cong et al. (2019b), aims to identify robust characters that are expected to remain valid as more specimens and species are sequenced.

We present character states using abbreviations for one of the four reference genomes: *Heliconius melpomene* (Linnaeus, 1758) (hm) (Davey et al. 2016), *Calephelis nemesis* (W. H. Edwards, 1871) (cne) (Cong et al. 2017b), *Calycopis cecrops* (Fabricius, 1793) (cce) (Cong et al. 2016), or *Cecropterus lyciades* (Geyer, 1832) (aly, due to its former placement in the genus *Achalarus* Scudder, 1872) (Shen et al. 2017). E.g., aly728.44.1:G672C means position 672 in exon 1 of gene 44 from scaffold 728 of the *Cecropterus lyciades* (Geyer, 1832) reference genome (Shen et al. 2017) is C, changed from G in the ancestor. When characters are given for the sister clade of the diagnosed taxon, the following notation is used: aly5294.20.2:A548A (not C), which means that position 548 in exon 2 of gene 20 on scaffold 5294 is occupied by the ancestral base pair A, which was changed to C in the sister clade (so it is not C in the diagnosed taxon). COI barcode positions follow the same format but lack a prefix ending in ':'. Complete exon sequences from the reference genomes, with diagnostic positions for new taxa highlighted in green, are provided in a supplementary file < https://osf.io/2vy8e/ >. By providing this link to the DNA sequences, the publication ensures that the characters used in diagnoses can be easily traced to their actual sequence data.

Whole genome shotgun datasets we obtained and used in this study are available from the NCBI database < https://www.ncbi.nlm.nih.gov/ > under BioProject PRJNA1253783. Associated BioSample records include locality data and other collection information for all specimens sequenced by us and shown in the trees. Tree figures list the following information for each specimen, separated by "|": taxon name with comments in square brackets, DNA sample code, type status, general locality, and year of collection ("old" if not dated and likely collected 100–150 years ago). Type status abbreviations are: HT holotype, LT lectotype, ST syntype, NT neotype, T type (could be ST, LT, paralectotype, or HT, status not investigated), PT paratype, AT allotype, PLT paralectotype; and if a synonym name is given (in parenthesis, preceded by "=", and in addition by "‡" for unavailable names), type status refers to the synonym. COI barcode sequences reported here have been deposited in GenBank with accessions PV549978–PV550072 and PV612660. Abbreviations or acronyms for collections are listed in the Acknowledgments section.

Chlosyne flavula blackmorei Pelham, 2008 and *Chlosyne palla sterope* (W. H. Edwards, 1870) may be sympatric in British Columbia, Canada

We proposed to treat *Chlosyne flavula* (W. Barnes & McDunnough, 1918) (type locality USA: Colorado, Garfield Co., Glenwood Springs) as a species distinct from *Chlosyne palla* (Boisduval, 1852) (type locality in USA: California, Plumas Co.) based on notable genetic differentiation and limited gene exchange between these two taxa (Zhang et al. 2023d). However, the ultimate evidence of distinction at the species level comes from finding two taxa in sympatry. Genomic sequencing of additional specimens from the Pacific Northwest reveals that the two species may be sympatric in Osoyoos, British Columbia, Canada, where a specimen of *Chlosyne flavula blackmorei* Pelham, 2008 (type locality Canada: British Columbia, Lytton) (NVG-24014H10, Fig. 1a) and a specimen of *Chlosyne palla sterope* (W. H. Edwards, 1870) (type locality in USA: Oregon, Wasco Co.) (NVG-24015A09, Fig. 1b) were collected by J. K. Jacob five days apart. However, the locality "Osoyoos" specified on the labels may refer to a general area only. Thus, further genomic sequencing to include various localities, especially from Idaho, will shed more light on the question about the sympatry of *C. palla* and *C. flavula*.

In the nuclear genomic tree, these two specimens from "Osoyoos" are placed in different clades corresponding to their species (Fig. 2 blue and red, highlighted yellow). Moreover, all additional specimens we sequenced are confidently attributed to their distinct clades by species and, within each species clade, by subspecies and their localities. Species clades are supported by bootstrap values of 100%, and no hybrids are observed. These additional results confirm that *Melitaea sterope* is a subspecies of *C. palla* and not of *Chlosyne acastus* (W. H. Edwards, 1874) (type locality in USA: Utah, probably Utah Co.) (Zhang et al. 2022c), and that *C. flavula* is a species distinct from *C. palla*.

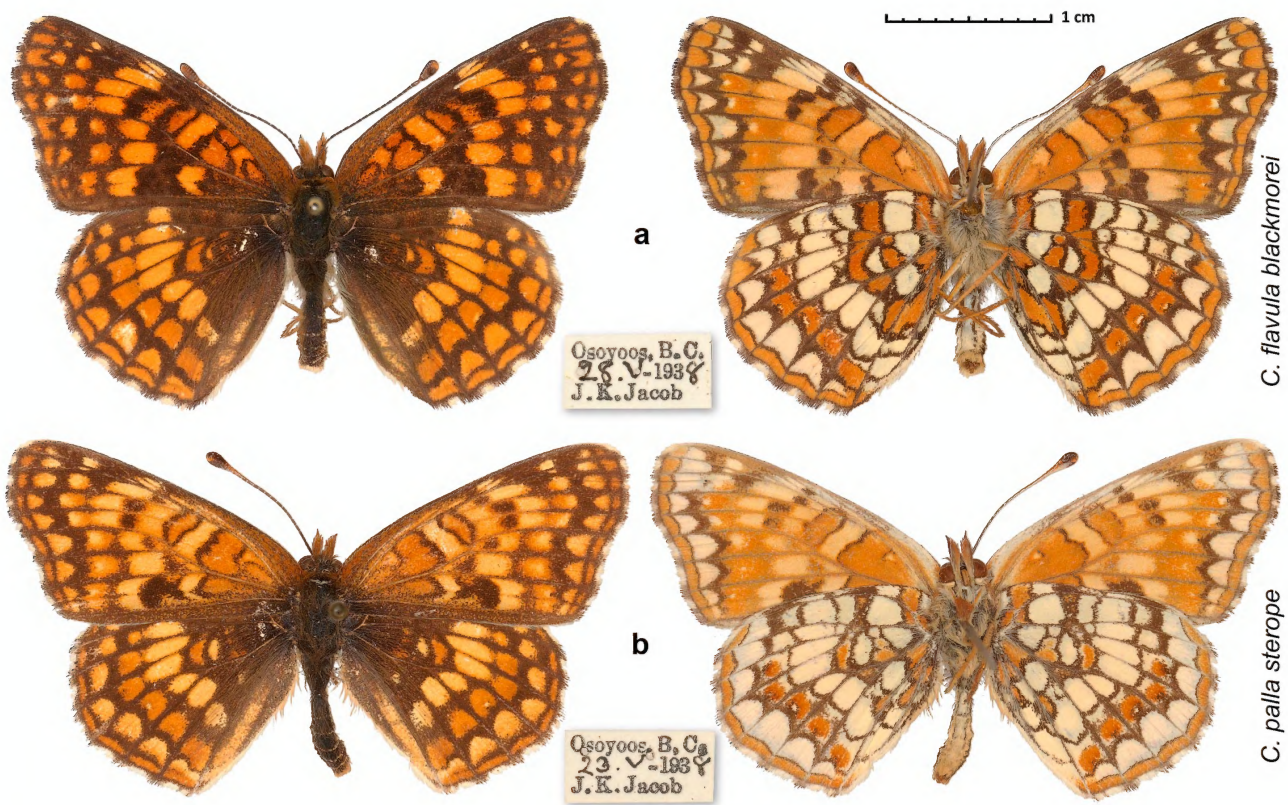


Fig. 1. Sequenced males of *Chlosyne* from Canada: British Columbia, Osoyoos [CNC], with their locality labels: **a)** *C. flavula blackmorei* NVG-24014H10 and **b)** *C. palla sterope* NVG-24015A09.

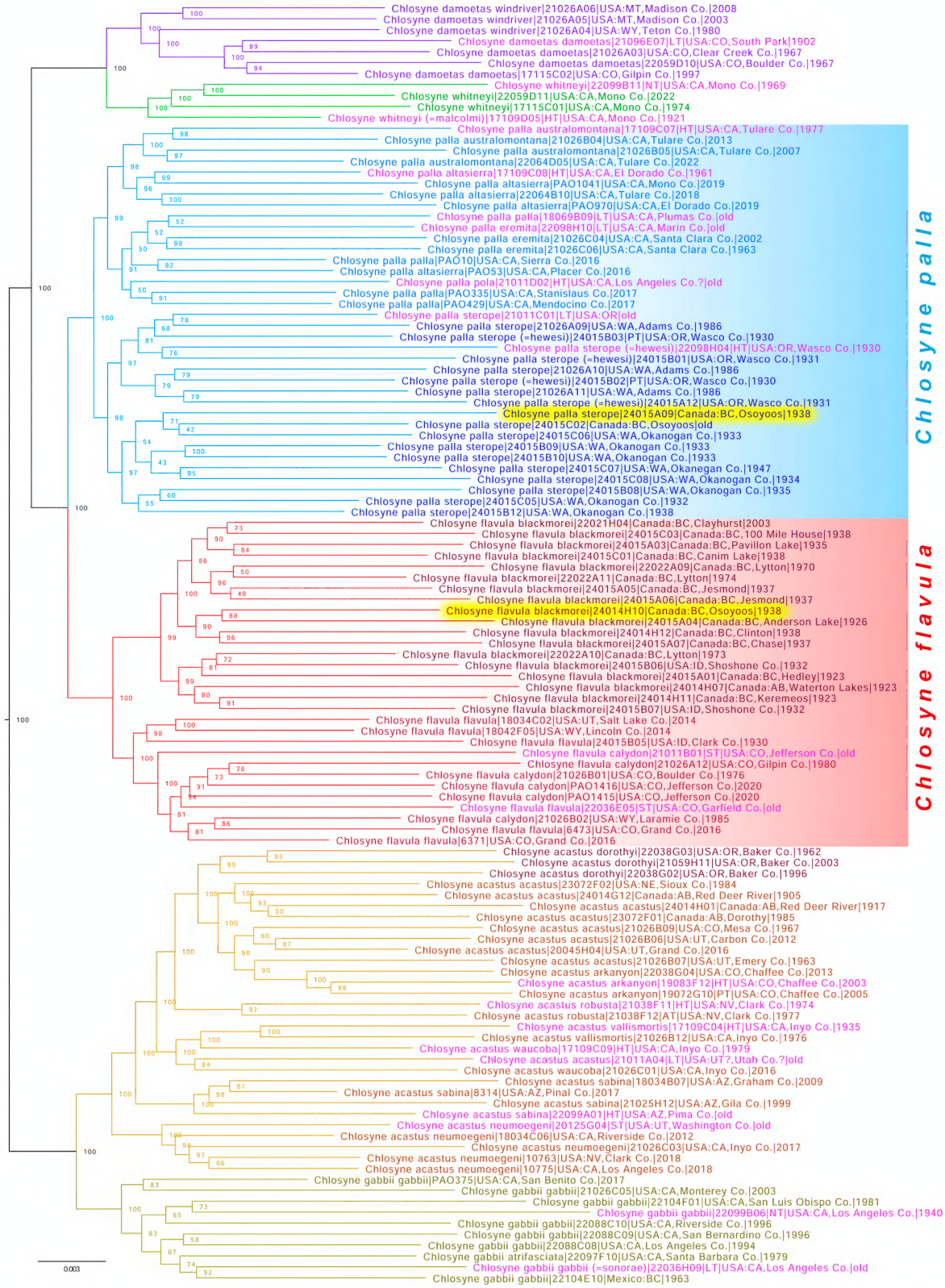

Chlosyne damoetas windriver|21026A06|USA:MT,Madison Co.|2008
Chlosyne damoetas windriver|21026A05|USA:MT,Madison Co.|2003
Chlosyne damoetas windriver|21026A04|USA:WY,Teton Co.|1980
Chlosyne damoetas damoetas|21096E07|LT|USA:CO,South Park|1902
Chlosyne damoetas damoetas|21026A03|USA:CO,Clear Creek Co.|1967
Chlosyne damoetas damoetas|22059D10|USA:CO,Boulder Co.|1967
Chlosyne damoetas damoetas|17115C02|USA:CO,Gilpin Co.|1997
Chlosyne whitneyi|22099B11|NT|USA:CA,Mono Co.|1969
Chlosyne whitneyi|22059D11|USA:CA,Mono Co.|2022
Chlosyne whitneyi|17115C01|USA:CA,Mono Co.|1974
Chlosyne whitneyi (=malcolmi)|17109D05|HT|USA:CA,Mono Co.|1921
Chlosyne palla australomontana|17109C07|HT|USA:CA,Tulare Co.|1977
Chlosyne palla australomontana|21026B04|USA:CA,Tulare Co.|2013
Chlosyne palla australomontana|21026B05|USA:CA,Tulare Co.|2007
Chlosyne palla australomontana|22064D05|USA:CA,Tulare Co.|2022
Chlosyne palla altasierra|17109C08|HT|USA:CA,El Dorado Co.|1961
Chlosyne palla altasierra|PAO1041|USA:CA,Mono Co.|2019
Chlosyne palla altasierra|22064B10|USA:CA,Tulare Co.|2018
Chlosyne palla altasierra|PAO970|USA:CA,El Dorado Co.|2019
Chlosyne palla palla|18069B09|LT|USA:CA,Plumas Co.|old
Chlosyne palla eremita|22098H10|LT|USA:CA,Marin Co.|old
Chlosyne palla eremita|21026C04|USA:CA,Santa Clara Co.|2002
Chlosyne palla eremita|21026C06|USA:CA,Santa Clara Co.|1963
Chlosyne palla palla|PAO10|USA:CA,Sierra Co.|2016
Chlosyne palla altasierra|PAO53|USA:CA,Placer Co.|2016
Chlosyne palla pola|21011D02|HT|USA:CA,Los Angeles Co.?|old
Chlosyne palla palla|PAO335|USA:CA,Stanislaus Co.|2017
Chlosyne palla palla|PAO429|USA:CA,Mendocino Co.|2017
Chlosyne palla sterope|21011C01|LT|USA:OR|old
Chlosyne palla sterope|21026A09|USA:WA,Adams Co.|1986
Chlosyne palla sterope (=hewesi)|24015B03|PT|USA:OR,Wasco Co.|1930
Chlosyne palla sterope (=hewesi)|22098H04|HT|USA:OR,Wasco Co.|1930
Chlosyne palla sterope (=hewesi)|24015B01|USA:OR,Wasco Co.|1931
Chlosyne palla sterope|21026A10|USA:WA,Adams Co.|1986
Chlosyne palla sterope (=hewesi)|24015B02|PT|USA:OR,Wasco Co.|1930
Chlosyne palla sterope|21026A11|USA:WA,Adams Co.|1986
Chlosyne palla sterope (=hewesi)|24015A12|USA:OR,Wasco Co.|1931
Chlosyne palla sterope|24015A09|Canada:BC,Osoyoos|1938
Chlosyne palla sterope|24015C02|Canada:BC,Osoyoos|old
Chlosyne palla sterope|24015C06|USA:WA,Okanogan Co.|1933
Chlosyne palla sterope|24015B09|USA:WA,Okanogan Co.|1933
Chlosyne palla sterope|24015B10|USA:WA,Okanogan Co.|1933
Chlosyne palla sterope|24015C07|USA:WA,Okanegan Co.|1947
Chlosyne palla sterope|24015C08|USA:WA,Okanogan Co.|1934
Chlosyne palla sterope|24015B08|USA:WA,Okanogan Co.|1935
Chlosyne palla sterope|24015C05|USA:WA,Okanogan Co.|1932
Chlosyne palla sterope|24015B12|USA:WA,Okanogan Co.|1938
Chlosyne flavula blackmorei|22021H04|Canada:BC,Clayhurst|2003
Chlosyne flavula blackmorei|24015C03|Canada:BC,100 Mile House|1938
Chlosyne flavula blackmorei|24015A03|Canada:BC,Pavillon Lake|1935
Chlosyne flavula blackmorei|24015C01|Canada:BC,Canim Lake|1938
Chlosyne flavula blackmorei|22022A09|Canada:BC,Lytton|1970
Chlosyne flavula blackmorei|22022A11|Canada:BC,Lytton|1974
Chlosyne flavula blackmorei|24015A05|Canada:BC,Jesmond|1937
Chlosyne flavula blackmorei|24015A06|Canada:BC,Jesmond|1937
Chlosyne flavula blackmorei|24014H10|Canada:BC,Osoyoos|1938
Chlosyne flavula blackmorei|24015A04|Canada:BC,Anderson Lake|1926
Chlosyne flavula blackmorei|24014H12|Canada:BC,Clinton|1938
Chlosyne flavula blackmorei|24015A07|Canada:BC,Chase|1937
Chlosyne flavula blackmorei|22022A10|Canada:BC,Lytton|1973
Chlosyne flavula blackmorei|24015B06|USA:ID,Shoshone Co.|1932
Chlosyne flavula blackmorei|24015A01|Canada:BC,Hedley|1923
Chlosyne flavula blackmorei|24014H07|Canada:AB,Waterton Lakes|1923
Chlosyne flavula blackmorei|24014H11|Canada:BC,Keremeos|1923
Chlosyne flavula blackmorei|24015B07|USA:ID,Shoshone Co.|1932
Chlosyne flavula flavula|18034C02|USA:UT,Salt Lake Co.|2014
Chlosyne flavula flavula|18042F05|USA:WY,Lincoln Co.|2014
Chlosyne flavula flavula|24015B05|USA:ID,Clark Co.|1930
Chlosyne flavula calydon|21011B01|ST|USA:CO,Jefferson Co.|old
Chlosyne flavula calydon|21026A12|USA:CO,Gilpin Co.|1980
Chlosyne flavula calydon|21026B01|USA:CO,Boulder Co.|1976
Chlosyne flavula calydon|PAO1416|USA:CO,Jefferson Co.|2020
Chlosyne flavula calydon|PAO1415|USA:CO,Jefferson Co.|2020
Chlosyne flavula flavula|22036E05|ST|USA:CO,Garfield Co.|old
Chlosyne flavula calydon|21026B02|USA:WY,Laramie Co.|1985
Chlosyne flavula flavula|6473|USA:CO,Grand Co.|2016
Chlosyne flavula flavula|6371|USA:CO,Grand Co.|2016
Chlosyne acastus dorothyi|22038G03|USA:OR,Baker Co.|1962
Chlosyne acastus dorothyi|21059H11|USA:OR,Baker Co.|2003
Chlosyne acastus dorothyi|22038G02|USA:OR,Baker Co.|1996
Chlosyne acastus acastus|23072F02|USA:NE,Sioux Co.|1984
Chlosyne acastus acastus|24014G12|Canada:AB,Red Deer River|1905
Chlosyne acastus acastus|24014H01|Canada:AB,Red Deer River|1917
Chlosyne acastus acastus|23072F01|Canada:AB,Dorothy|1985
Chlosyne acastus acastus|21026B09|USA:CO,Mesa Co.|1967
Chlosyne acastus acastus|21026B06|USA:UT,Carbon Co.|2012
Chlosyne acastus acastus|20045H04|USA:UT,Grand Co.|2016
Chlosyne acastus acastus|21026B07|USA:UT,Emery Co.|1963
Chlosyne acastus arkanyon|22038G04|USA:CO,Chaffee Co.|2013
Chlosyne acastus arkanyon|19083F12|HT|USA:CO,Chaffee Co.|2003
Chlosyne acastus arkanyon|19072G10|PT|USA:CO,Chaffee Co.|2005
Chlosyne acastus robusta|21038F11|HT|USA:NV,Clark Co.|1974
Chlosyne acastus robusta|21038F12|AT|USA:NV,Clark Co.|1977
Chlosyne acastus vallismortis|17109C04|HT|USA:CA,Inyo Co.|1935
Chlosyne acastus vallismortis|21026B12|USA:CA,Inyo Co.|1976
Chlosyne acastus waucoba|17109C09|HT|USA:CA,Inyo Co.|1979
Chlosyne acastus acastus|21011A04|LT|USA:UT?,Utah Co.?|old
Chlosyne acastus waucoba|21026C01|USA:CA,Inyo Co.|2016
Chlosyne acastus sabina|18034B07|USA:AZ,Graham Co.|2009
Chlosyne acastus sabina|8314|USA:AZ,Pinal Co.|2017
Chlosyne acastus sabina|21025H12|USA:AZ,Gila Co.|1999
Chlosyne acastus sabina|22099A01|HT|USA:AZ,Pima Co.|old
Chlosyne acastus neumoegeni|20125G04|ST|USA:UT,Washington Co.|old
Chlosyne acastus neumoegeni|18034C06|USA:CA,Riverside Co.|2012
Chlosyne acastus neumoegeni|21026C03|USA:CA,Inyo Co.|2017
Chlosyne acastus neumoegeni|10763|USA:NV,Clark Co.|2018
Chlosyne acastus neumoegeni|10775|USA:CA,Los Angeles Co.|2018
Chlosyne gabbii gabbii|PAO375|USA:CA,San Benito Co.|2017
Chlosyne gabbii gabbii|21026C05|USA:CA,Monterey Co.|2003
Chlosyne gabbii gabbii|22104F01|USA:CA,San Luis Obispo Co.|1981
Chlosyne gabbii gabbii|22099B06|NT|USA:CA,Los Angeles Co.|1940
Chlosyne gabbii gabbii|22088C10|USA:CA,Riverside Co.|1996
Chlosyne gabbii gabbii|22088C09|USA:CA,San Bernardino Co.|1996
Chlosyne gabbii gabbii|22088C08|USA:CA,Los Angeles Co.|1994
Chlosyne gabbii atrifasciata|22097F10|USA:CA,Santa Barbara Co.|1979
Chlosyne gabbii gabbii (=sonorae)|22036H09|LT|USA:CA,Los Angeles Co.|old
Chlosyne gabbii gabbii|22104E10|Mexico:BC|1963
0.003
Chlosyne palla
Chlosyne flavula

Fig. 2. Phylogenetic trees of several *Chlosyne* species inferred from protein-coding regions in the nuclear genome (autosomes), based on 1,471,464 positions. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species are colored differently: *C. damoetas* (purple), *C. whitneyi* (green), *C. palla* (blue with *C. palla sterope* labeled in darker color), *C. flavula* (red with *C flavula blackmorei* labeled in darker color), *C. acastus* (orange with *C. acastus dorothyi* labeled in darker color), and *C. gabbii* (olive). Primary type specimens are labeled in magenta, and possibly sympatric specimens of *C. flavula* and *C. palla* shown in Fig. 1 are highlighted in yellow.

Erebia (*Erebia*) *pawloskii* Ménétriés, 1859 is confirmed as a species distinct from *Erebia theano* (Tauscher, 1806) and *Erebia stubbendorfii* Ménétriés, 1847

Nuclear genome phylogeny reveals that *Erebia* (*Erebia*) *theano* (Tauscher, 1806) (type locality in Altai Mts.) (Fig. 3a brown), *Erebia* (*Erebia*) *stubbendorfii* Ménétriés, 1847 (type locality Russia: Kansk) (Fig. 3a olive), and *Erebia* (*Erebia*) *pawloskii* Ménétriés, 1859 (type locality in Russia: Sakha) (Fig. 3a purple, blue, magenta, green, dark blue, and cyan, with the nominate in blue), form strongly supported (100% ultrafast bootstrap (Minh et al. 2013)) clades genetically differentiated at the species level, e.g., their F_{st} values are: 0.36 (*E. theano* and *E. stubbendorfii*), 0.36 (*E. theano* and *E. pawloskii*), and 0.28 (*E. stubbendorfii* and *E. pawloskii*). Therefore, genomic analysis supports the three distinct species hypothesis (Lukhtanov and Lukhtanov 1994; Gorbunov 2001) and suggests that the name *stubbendorfii* should not be applied to *E. pawloskii*. Curiously, mitochondrial genome phylogeny is different, and reveals two major haplotypes for these species, split by geography: the Old World haplotype (including the North Slope of Alaska, USA) and the New World haplotype (the rest of Alaska, Canada, and the US) (Fig. 3b). Similar evolutionary scenarios, likely resulting from mitochondrial introgression, are known in other butterfly groups, such as *Junonia* Hübner, [1819] (Gemmell and Marcus 2015), and offer a cautionary lesson against relying solely on mitochondrial data (e.g., COI barcodes) to address species delimitation.

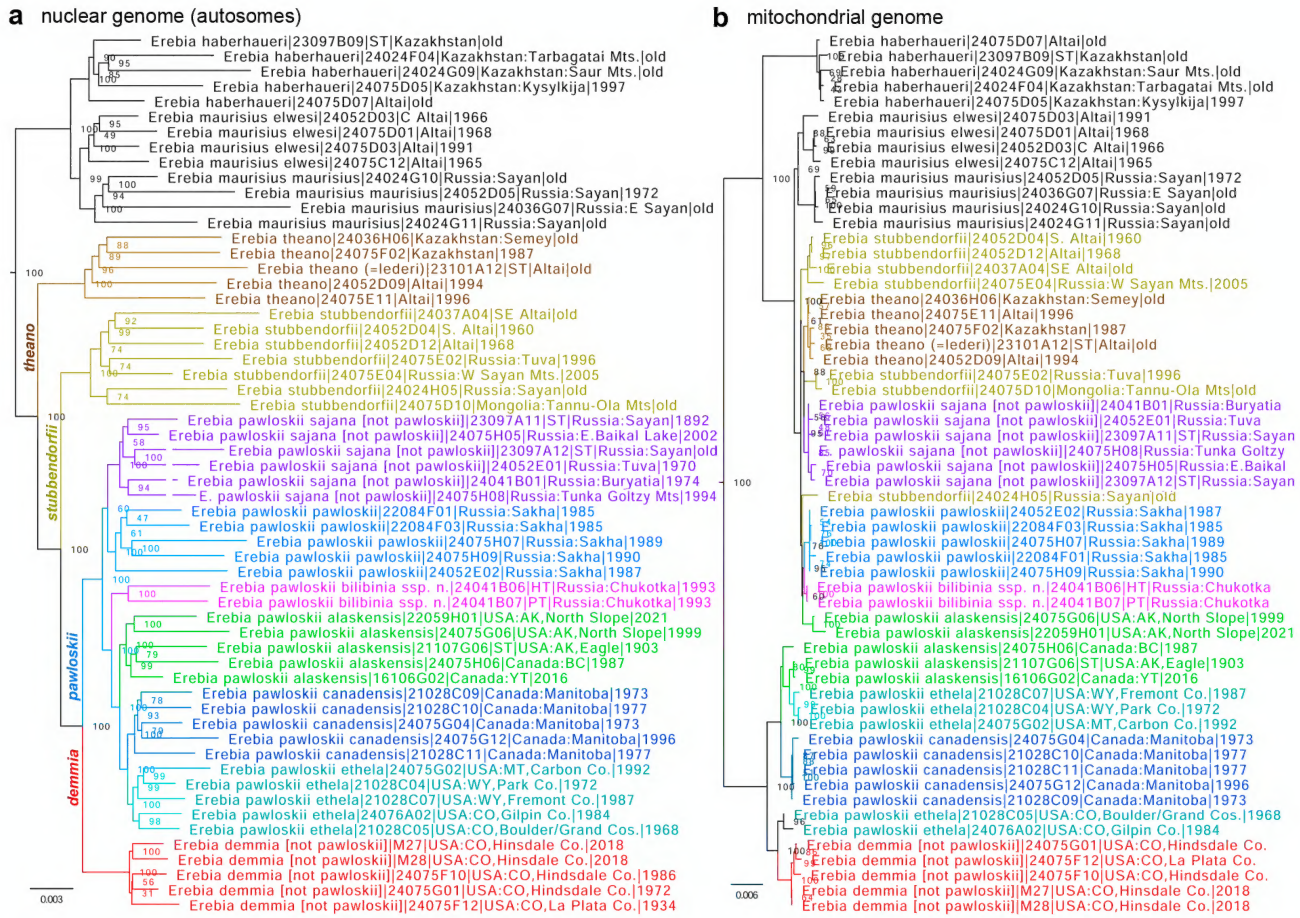


Fig. 3. Phylogenetic trees of selected *Erebia* (*Erebia*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 415,959 positions, and **b)** the mitochondrial genome. Different species and subspecies are colored differently: *E. theano* (brown), *E. stubbendorfii* (olive), *E. pawloskii sajana* **stat. rest.** (purple), *E. pawloskii pawloskii* (blue), *E. pawloskii bilibinia* (magenta), *E. pawloskii alaskensis* (green), *E. pawloskii canadensis* (dark blue), *E. pawloskii ethela* W. H. Edwards, 1891 (cyan), and *E. demmia* **stat. nov.** (red). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Gaps in terminal branches indicate that a segment of a tree was cut out to reduce its horizontal dimension (to allow an increase in the font size), i.e., a branch with a gap is longer than shown.

Erebia (*Erebia*) *demmia* B. Warren, 1936, stat. nov. is a species distinct from *Erebia* (*Erebia*) *pawloskii* Ménétriés, 1859

Originally proposed as a subspecies of *Erebia* (*Erebia*) *theano* (Tauscher, 1806) (type locality in Altai Mts.), and currently treated as a subspecies of *Erebia* (*Erebia*) *pawloskii* Ménétriés, 1859 (type locality in Russia: Sakha), *Erebia theano demmia* Warren, 1936 (type locality in USA: Colorado, San Juan Mountains) is genetically differentiated from them at the species level (Fig. 3a red), e.g., F_{st}/G_{min} statistics for the phylogenetically closest pair (*E. theano demmia* and *E. pawloskii*) are 0.34/0.015. Therefore, we propose that *Erebia* (*Erebia*) *demmia* B. Warren, 1936, **stat. nov.** is a species distinct from *Erebia* (*Erebia*) *pawloskii* Ménétriés, 1859.

Erebia (*Erebia*) *pawloskii sajana* Staudinger, 1894, stat. rest. is a valid subspecies

At times, synonymized with *Erebia* (*Erebia*) *pawloskii pawloskii* Ménétriés, 1859 (type locality in Russia: Sakha), *Erebia pawlowskyi* [sic] var. *sajana* Staudinger, 1894 (type locality in Russia: Buryatia, East Sayan) forms a distinct clade in both genomic trees (Fig. 3 purple) genetically differentiated from others at the subspecies level (e.g., Fig. 3 purple vs. blue). Therefore, we treat *Erebia* (*Erebia*) *pawloskii sajana* Staudinger, 1894, **stat. rest.** as a valid subspecies, not a synonym of *E. pawloskii pawloskii*.

Erebia (*Erebia*) *pawloskii bilibinia* Grishin, new subspecies

http://zoobank.org/79EA8344-F03A-4D4C-A7D4-F3095814D506

(Figs. 3 part, 4)

Definition and diagnosis. Genomic analysis of *Erebia* (*Erebia*) *pawloskii* Ménétriés, 1859 (type locality in Russia: Sakha) specimens reveals a clade of a pair from Chukotka, Russia, not monophyletic with any

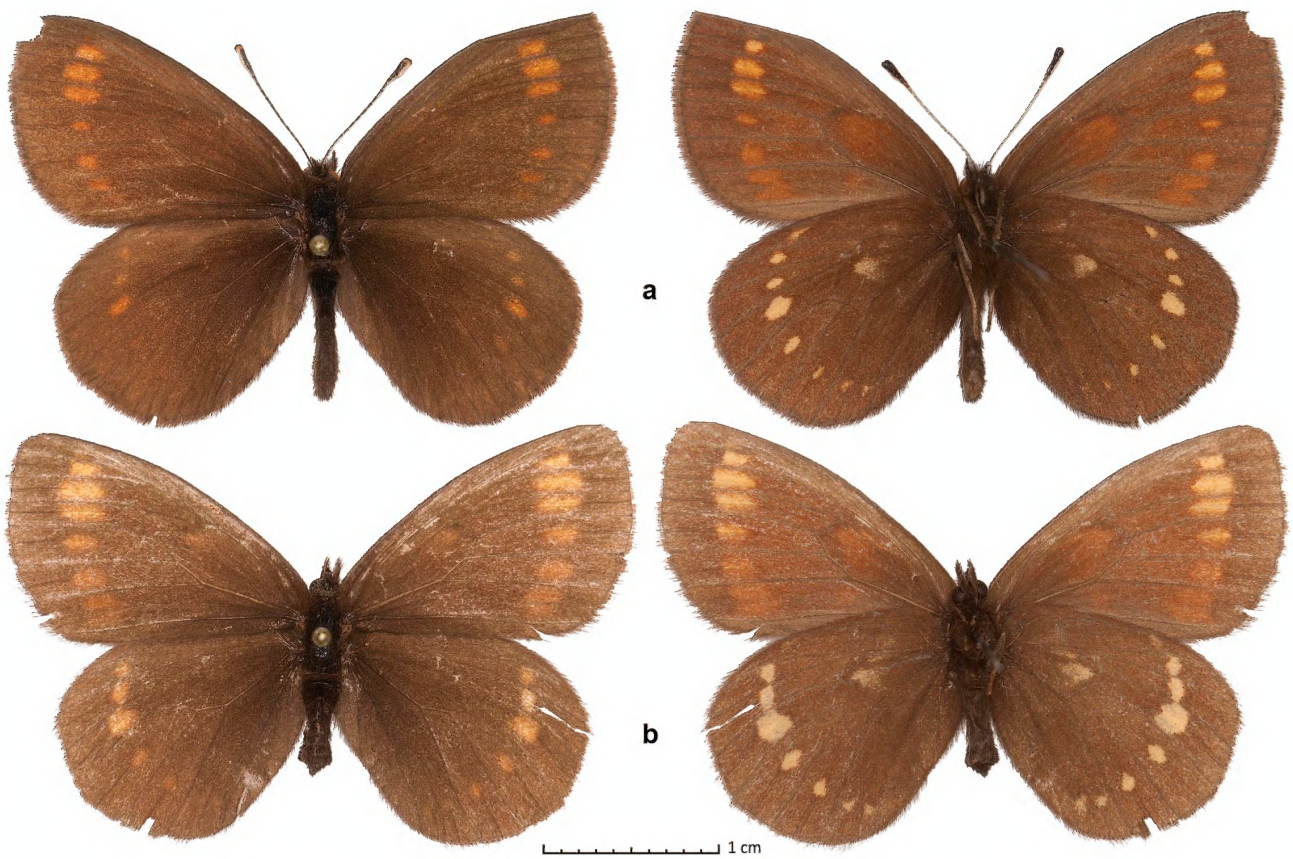


Fig. 4. *Erebia* (*Erebia*) *pawloskii bilibinia* **ssp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-24041B06 and **b)** paratype ♀ NVG-24041B07.

known subspecies and genetically differentiated from them (Fig. 3 magenta). Therefore, this clade represents a new subspecies. It differs by smaller orange and cream spots than in most other subspecies (except the two mentioned next), the spots are vestigial in the posterior 2/3rd of the hindwing of a male, but larger ventral hindwing cream spots than in *Erebia pawloskii alaskensis* W. Holland, 1900 (type locality in USA: Alaska) and *Erebia pawloskii canadensis* B. Warren, 1931 (type locality in Canada: Manitoba). Due to unexplored individual variation in this subspecies, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: hm2021401-RA.2:C36T, hm2021401-RA.2:T87C, hm2004829-RA.3:C54T, hm2007306-RA.8:A114G, hm2018041-RA.1:A456G. However, this taxon does not differ from other subspecies and even related species in the COI barcode because the mitochondrial genome seems to introgress among the relatives (Fig. 3b).

Barcode sequence of the holotype. Sample NVG-24041B06, GenBank PV549978, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCAGGTATAGTAGGTACATCTCTCAGTTTAATTATTCGAACAGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGTAATTGACTTATTCCTATTATATTAGGAGCCCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGACTCCTTCCCCCCTCTTTAATTTTATTAATTTCAAGTAGTATTGTAGAAAATGGTGCTGGTACAGGATGAACGGTTTATCCCCCCCTTTCATCTAATATTGC
TCACAGTGGATCTTCTGTTGATTTAGCAATTTTCTCTTTACATTTAGCTGGAATTTCATCAATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAGTATATCT
TATGATCAAATACCATTATTTGTTTGAGCTGTTGGAATTACAGCATTATTATTATTACTCTCTCTACCTGTATTAGCTGGAGCTATTACAATACTTCTTACAGATCGAAATTTAAACACCT
CTTTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS), illustrated in Fig. 4a, bears the following four printed rectangular labels, three white: [Russland, E.-Sibiria | Chukotka, Bilibino | VII. 1993 | leg. Karpov], [ex coll. W. Eckweiler | SMNS-Lep. 2005 – 07], [DNA sample ID: | NVG-24041B06 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Erebia pawloskii | bilibinia Grishin]. **Paratype:** 1♀ NVG-24041B07 the same data as the holotype (Fig. 4b).

Type locality. Russia: Chukotka, Bilibino.

Etymology. The name is given for the type locality and is treated as a feminine noun in apposition.

Distribution. Currently known only from Chukotka in Russia.

Family Riodinidae Grote, 1895 (1827)

Balonca F. Moore, 1901 is a valid subgenus of *Dodona* Hewitson, 1861

Genomic analysis of *Dodona* Hewitson, 1861 (type species *Melitaea durga* Kollar, 1844) reveals that the genus partitions into four prominent clades genetically differentiated at the subgenus level (Fig. 5). One of these clades corresponds to *Balonca* F. Moore, 1901 (type species *Dodona deodata* Hewitson, 1876), currently regarded as a junior subjective synonym of *Dodona*. *Dodona* and *Balonca* type species differ by 6.8% (45 bp) in their COI barcodes. Therefore, we propose to treat *Balonca* F. Moore, 1901, **stat. nov.** as

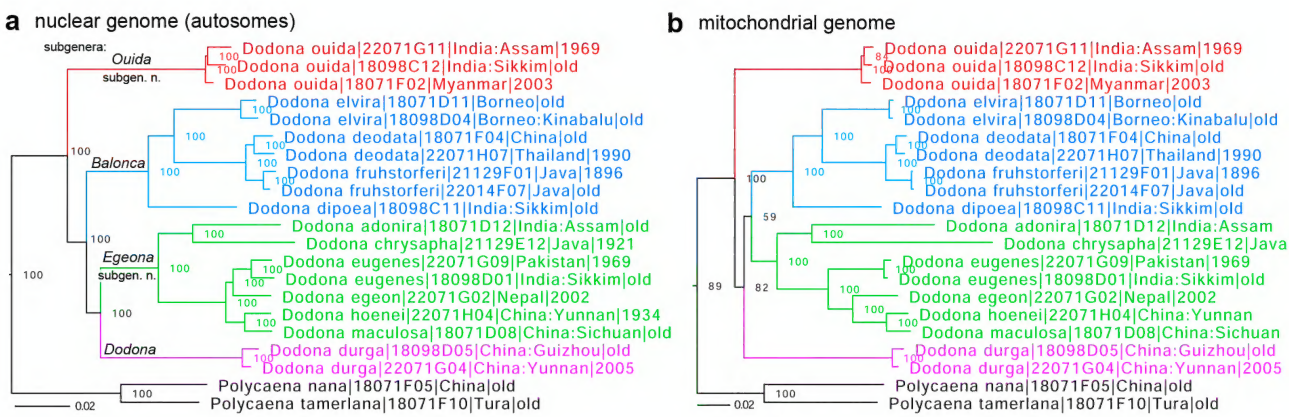


Fig. 5. Phylogenetic trees of selected *Dodona* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,488,244 positions, and **b)** the mitochondrial genome. Different subgenera are colored differently: *Ouida* **subgen. n.** (red), *Balonca* (blue), *Egeona* **subgen. n.** (green), and *Dodona* (magenta). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

a subgenus of *Dodona* Hewitson, 1861. The two other clades do not include type species of any available genus group names and, therefore, correspond to the new subgenera described below.

Ouida Grishin, new subgenus

http://zoobank.org/54C8B894-E6E2-443F-9C01-2C6A367B5CFC

Type species. *Dodona ouida* Hewitson, 1866.

Definition. Genome-based phylogeny reveals that *Dodona* Hewitson, 1861 (type species *Melitaea durga* Kollar, 1844) splits into four clades that we define as subgenera (Fig. 5). Two of them have names: *Dodona*, which consists of only the type species, and *Balonca* F. Moore, 1901 (type species *Dodona deodata* Hewitson, 1876), which includes all other species not placed in the two new subgenera. The clade with *Dodona ouida* Hewitson, 1866 (type locality in India: Darjeeling) (Fig. 5 red) is sister to all other *Dodona* species and represents the first new subgenus. This new subgenus differs from its relatives by the following combination of characters: brown wings with three (not four) continuous orange stripes on the forewing (submarginal, discal, and basal) in males, and a single cream forewing discal band in females; and the ventral hindwing having a black spot by the costa in the middle with a white spot distad merged with it. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cne246.3.1:A1743G, cne792.27.11:G1335C, cne14967.2.1:A330T, cne14967.2.1:T342C, cne14967.2.1:C358A; and in COI barcode: A31T, T59C, A79T, T364C, A469T, 499A (not T).

Etymology. The name of the subgenus is tautonymous with its type species name and is a feminine noun in the nominative singular.

Species included. Only the type species (i.e., *Dodona ouida* Hewitson, 1866).

Parent taxon. Genus *Dodona* Hewitson, 1861.

Egeona Grishin, new subgenus

http://zoobank.org/BFF752DF-DA63-4043-91F6-34E579F956F8

Type species. *Taxila egeon* Westwood, 1851.

Definition. This is the second new subgenus of *Dodona* Hewitson, 1861 (type species *Melitaea durga* Kollar, 1844) (see above for discussions) (Fig. 5 green) that is sister to the nominal subgenus (Fig. 5 magenta). COI barcodes between these sister taxa differ by 7.3% (48 bp). This new subgenus differs from its relatives by the following combination of characters: the phallus is usually longer and stronger curved, the phallobase is straighter and the connection between the phallus and phallobase is less bent; males have brown wings with orange spots and stripes above (four stripes on the forewing: the apical stripe—which is sometimes vestigial—not merged with the submarginal stripe) but without white areas and stripes characteristics of *Balonca* and with wings and orange spots less round and spots less uniform than in the subgenus *Dodona*, and differs from several similar-looking species of *Balonca* either by more extensive orange coloration, especially of the ventral side, or by not having brown framing on the basal side of pale hindwing streaks. For genitalia illustrations of some representative species in the new subgenus, see Wu et al. (2018). In DNA, a combination of the following characters is diagnostic in the nuclear genome: cne3991.3.1:T363C, cne3991.3.1:T384C, cne9860.2.4:C37T, cne1134.1.1:A336G, cne3461.1.15:C2524A; and in COI barcode: T127A or T463C, A202C or T206C, T479T, T484T, T571C or T574A, T533T.

Etymology. The name is formed from the name of the type species and is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Taxila egeon* Westwood, 1851), *Dodona adonira* Hewitson, 1866, *Dodona chrysapha* Fruhstorfer, 1910, *Dodona eugenes* H. Bates, 1867, *Dodona formosana* Matsumura, 1919, *Dodona hoenei* Forster, 1951, *Dodona maculosa* Leech, 1890, *Dodona phuongi* Monastyrskii & Devyatkin, 2000, *Dodona speciosa* Monastyrskii & Devyatkin, 2000, and *Dodona windu* Fruhstorfer, 1894, including their subspecies and synonyms.

Parent taxon. Genus *Dodona* Hewitson, 1861.

Lasaia cola Grishin, new species

http://zoobank.org/83817CD8-BC22-4AA1-BF5C-7F07CA4DF9D7

(Figs. 6 part, 7, 8b)

Definition and diagnosis. Nuclear genome analysis of *Lasaia* H. Bates, 1868 (type species *Papilio meris* Stoll, 1781) reveals a clade (Fig. 6a red) that is sister to both *Lasaia sula* Staudinger, 1888 (type locality in Honduras) (Fig. 6 blue) and *Lasaia peninsularis* Clench, 1972 (type locality in Mexico: Veracruz) (Fig. 6a purple), thus representing a new species. The three species (the new one, *L. sula*, and *L. peninsularis*) are genetically differentiated from each other to a similar degree in the nuclear genome (Fig. 6a) (F_{st} 0.37 and 0.44 between the new one and *L. sula* and *L. peninsularis*, respectively) but do not strongly differ in the mitochondrial genome (Fig. 6b) and, consequently, also in the COI barcode. The new species differs from its relatives by males having better developed dark spots and dashes, the hindwing with stronger developed dark dashes, similarly to the forewing (weaker than on the forewing or absent dashes in both *L. sula* and *L. peninsularis*), and some specimens having less blue above, greyer, thus somewhat resembling *Lasaia maria maria* Clench, 1972 (type locality in Mexico: Jalisco) and *Lasaia sessilis* Schaus, 1890 (type locality in Mexico: Veracruz), but are paler and patterned more like *L. sula*. In male genitalia (Fig. 8), the transtilla (McAlpine 1971) is pointed in the middle as in *L. peninsularis* and not flattened as in *L. sula* (Fig. 8 green arrow 1); lateral lobes of the transtilla are narrower than in *L. sula* and are more similar to *L. peninsularis* (Fig. 8 green arrow 2), if not smaller; and the scobinate bulla (Clench 1972) (Fig. 8 green arrow 3) is more robust than in the other two species. Due to the cryptic nature of this species and

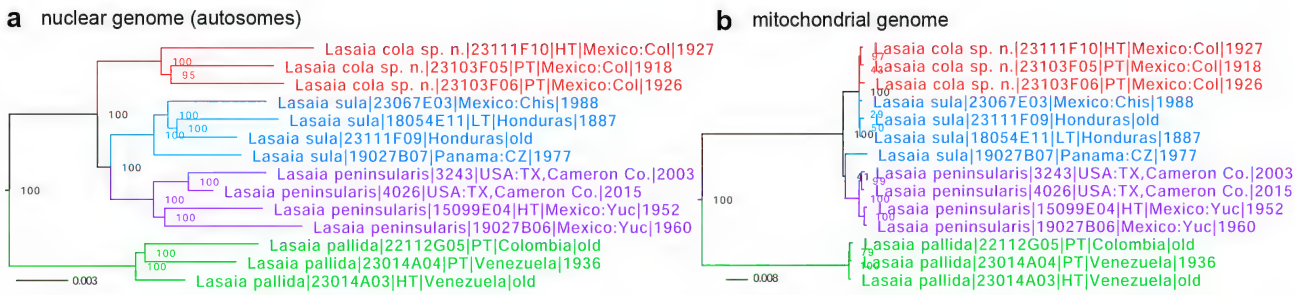


Fig. 6. Phylogenetic trees of selected *Lasaia* species (*L. sula* species group) constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,871,172 positions, and **b)** the mitochondrial genome. Different species are colored differently: *L. cola* **sp. n.** (red), *L. sula* (blue), *L. peninsularis* (purple), and *L. pallida* Grishin, 2024 (green). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

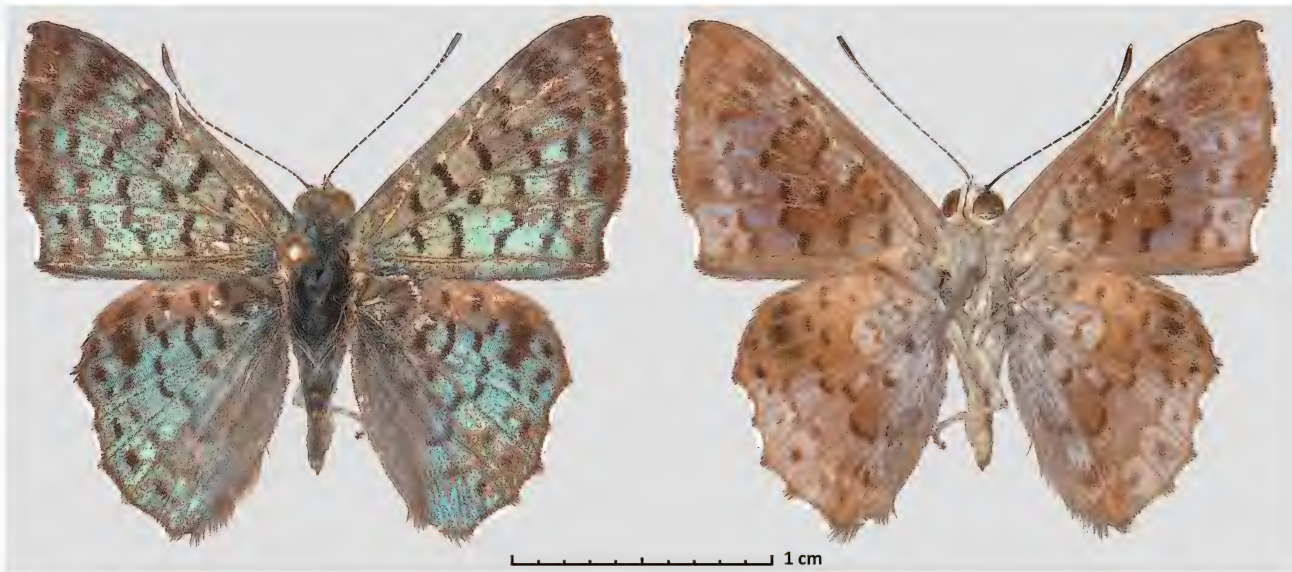


Fig. 7. *Lasaia cola* **sp. n.** holotype ♂ NVG-23103F05 in dorsal (left) and ventral (right) views, data in text.

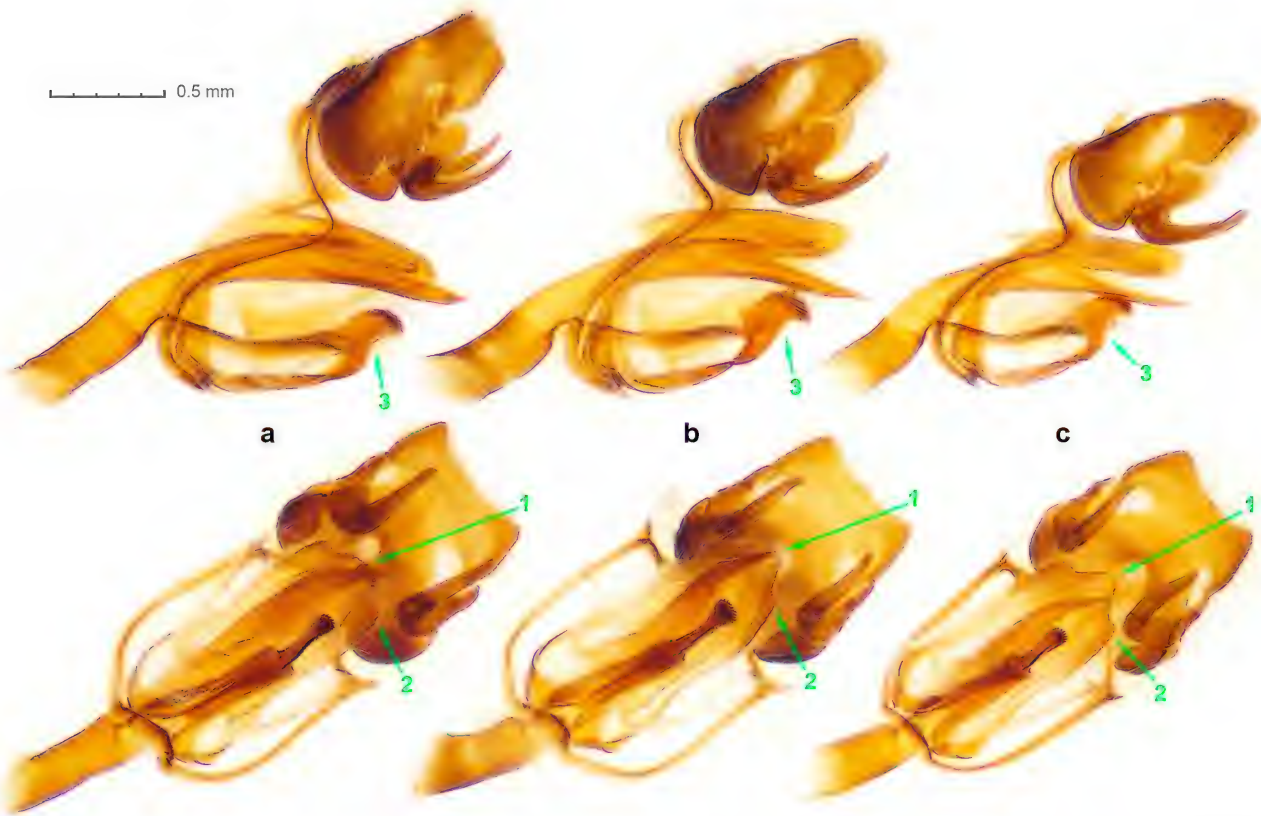


Fig. 8. Male genitalia of *Lasaia* in left lateral (above each panel letter) and ventral (below each panel letter) views, data in text or below [MGCL]: **a)** *L. sula* NVG-24081A11 from Costa Rica, Guanacaste, 6 mi S and 6 mi W of Canas, Reserva Forestal Taboga, GPS 10.317, −85.150, 10-Jul-1968; **b)** *L. cola* **sp. n.** paratype NVG-24079H06 from Mexico: Colima; **c)** *L. peninsulais* NVG-25014D04 from USA: Texas, Hidalgo Co., Rio Rico Rd. near Relampago, 18-Nov-1998, E. C. Knudson leg. Green arrows point to characters useful for identification of these species, numbered 1 to 3, details in text.

unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne2812.5.8:A69T, cne28857.1.4:G42A, cne28857.1.4:A65G, cne8137.3.6:C54T, cne8137.3.6:C66T. The COI barcode does not differ for *L. sula*.

Barcode sequence of the holotype. Sample NVG-23103F05, GenBank PV549979, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACATCATTAAGTTTATTAATTCGTATAGAATTAGGTATACCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTTGGTAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCATCTTTATTTCTATTAATTTCAAGAAGTATTGTAGAAAATGGAGCAGGAACTGGTTGAACAGTTTATCCCCCTTTATCTTCTAATATTGC
CCACGGAGGATCCTCAGTAGATTTAGCTATTTTCTCTCTTCATTTAGCAGGAATTTCTTCAATTTTAGGAGCCATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCATTATTCGTATGATCCGTTGGTATTACTGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACAT
CTTTTTTTGATCCAGCAGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Fig. 7, bears the following four rectangular labels (1st handwritten, others printed), three white: [MEXICO: Colima | Comala 2100 ft. | 1.X.1967 | R.G.Wind], [R.G. Wind, leg. | Gift of F.M.Brown | C.M. Acc. 23123], [DNA sample ID: | NVG-23111F10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Lasaia cola | Grishin]. **Paratypes:** 2♂♂ and 1♀ from Mexico, Colima: 1♂ NVG-24079H06 (leg DNA extraction, sequenced), NVG-25014D03 (abdomen DNA extraction and dissection) La Salada, 1000 ft, 4-Jan-1968, Robert G. Wind leg., genitalia NVG250517-02 (Fig. 8b) [MGCL] and (no locality details) [SMF]: 1♂ NVG-23103F05 May-1918 and 1♀ NVG-23103F06 Oct-1926.

Type locality. Mexico: Colima, Comala, elevation 2100 ft.

Etymology. The name is formed from the type locality in *Col*[im]*a* and is a feminine noun in apposition.

Distribution. Currently known only from Colima in Mexico.

Comment. In *Lasaia*, valvae are partly (and weakly) sclerotized and are flexible, semi-transparent side flaps (with sparse setae) on the sides of the scobinate bulla (Clench 1972), as seen in Fig. 8a, ventral view.

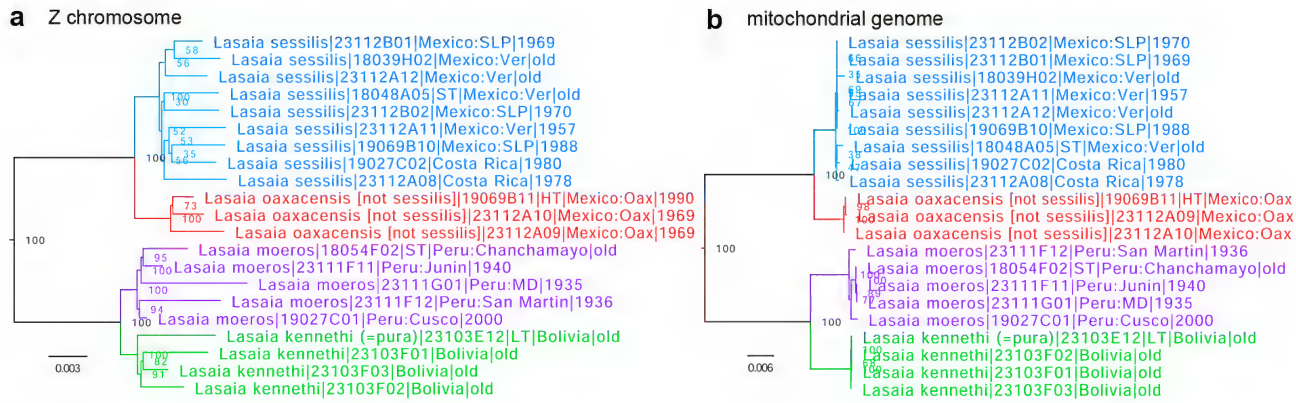


Fig. 9. Phylogenetic trees of *Lasaia sessilis* and relatives inferred from protein-coding regions in: **a)** the Z chromosome, based on 234,846 positions, and **b)** the mitochondrial genome. Different species are colored differently: *L. sessilis* (blue), *L. oaxacensis* **stat. nov.** (red), *L. moeros* (purple), and *L. kennethi* (green). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

Lasaia oaxacensis Grishin, 2024, stat. nov. is a species distinct from *Lasaia sessilis* Schaus, 1890

Lasaia sessilis oaxacensis Grishin, 2024 (type locality in Mexico: Oaxaca) was described from a single specimen that was distinct from but closely related to *Lasaia sessilis* Schaus, 1890 (type locality in Mexico: Veracruz, Coatepec, syntype sequenced as NVG-18048A05). We found and sequenced two more specimens of *L. sessilis oaxacensis* and were able to carry out more detailed genomic comparison between this taxon and the nominate subspecies (Fig. 9), leading to F_{st} (genetic differentiation) and G_{min} (introgression) statistics (computed on the Z chromosome) of 0.42 and 0.01, respectively. These numbers are in better agreement with species-level differences between the two taxa. Sequenced specimens of *L. sessilis sessilis* from distant localities from Mexico (San Luis Potosí and Veracruz) to Costa Rica cluster very closely with each other in genomic trees (Fig. 9 blue) and are more distant from *L. sessilis oaxacensis*. Moreover, the genetic differentiation in the Z chromosome is larger between *L. sessilis sessilis* and *L. sessilis oaxacensis* (Fig. 9a blue and red) than between the two species, *Lasaia moeros* Staudinger, 1888 (type locality in Peru: Chanchamayo) and *Lasaia kennethi* Weeks, 1901 (type locality in Bolivia) (Fig. 9a purple and green). For all these reasons, we propose that *Lasaia oaxacensis* Grishin, 2024, **stat. nov.** is a species distinct from *Lasaia sessilis* Schaus, 1890.

Locris Grishin, new subgenus

http://zoobank.org/F0535E1E-FBA7-45EC-AFA8-345BD6BC7C75

Type species. *Lasaia oileus* Godman, 1903.

Definition. Genomic phylogeny of *Lasaia* Bates, 1868 (type species *Papilio meris* Stoll, 1781) reveals that *Lasaia oileus* Godman, 1903 (type locality in Paraguay) (Fig. 10 red) is sister to all other species and is strongly differentiated from them genetically at the subgenus level (Fig. 10 blue vs. red); e.g., their COI barcodes differ by 7.4–8.4% (49–55 bp) and, therefore, the clade with *L. oileus* represents a new subgenus. This new subgenus keys to 10a in the *Lasaia* key of Clench (1972) and corresponds, in part, to the "E. *oileus* group" of Clench inherited from the "Cohort 3. Oileiformis" of Stichel (1910-1911), who described its phenotypic characters in detail, first, for the genus *Lasaia*, and second for "Oileiformis", which he has not proposed a genus group name for, but characterized as "ground color of the wings above in both sexes blackish or brown," in contrast to bluish, greenish, or grayish tones in males of other *Lasaia*. To this definition, the following should be added: smaller size than its congeners; white spots in several cells by the forewing costa about 2/3 from the base and pale submarginal overscaling on the hindwing above between dark-brown spots and dots; and prominent white segments on the fringes, particularly on the hindwing. In DNA, a combination of the following characters is diagnostic in the nuclear genome:

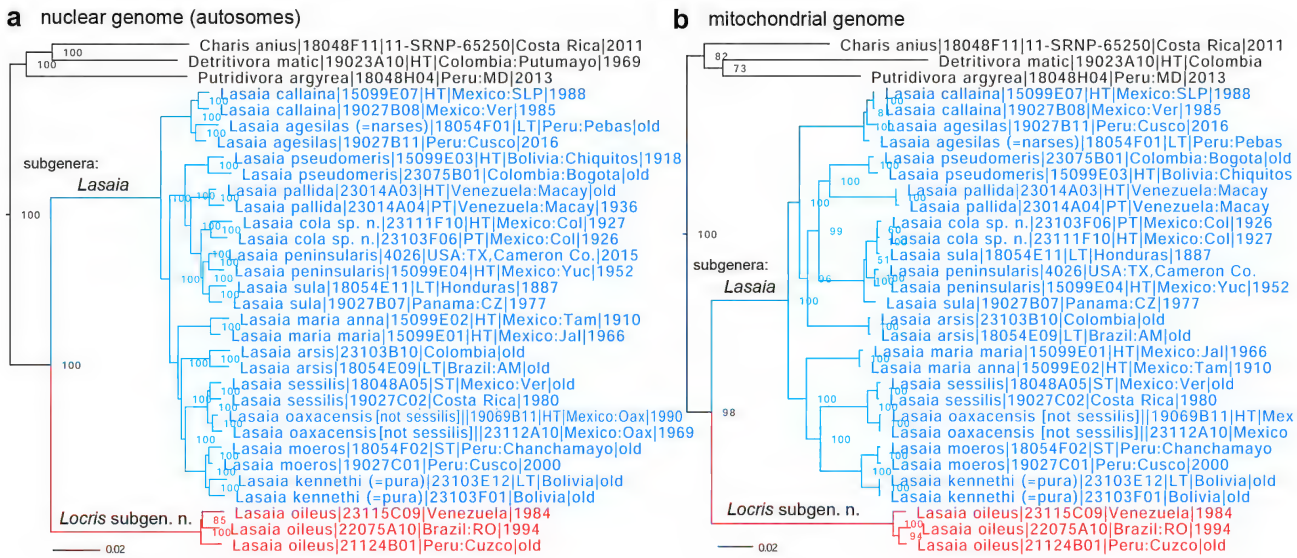


Fig. 10. Phylogenetic trees of *Lasaia* and relatives inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 6,309,384 positions, and **b)** the mitochondrial genome, showing subgenera *Lasaia* (blue) and *Locris* **subgen. n.** (red) labeled above corresponding branches. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

cne657.9.2:A465C, cne8314.8.1:A224G, cne7888.2.6:G30A, cne5774.10.1:T414C, cne5774.10.1:T426A; and in COI barcode: A22T, T121A, T418C, T374G, A625T, A637T.

Etymology. Oileus (Ὀϊλεύς) was the king of Locris, a region in ancient Greece. The name is a masculine noun in the nominative singular.

Species included. Only the type species (i.e., *Lasaia oileus* Godman, 1903).

Parent taxon. Genus *Lasaia* H. Bates, 1868.

Curvie yucatanensis (Godman & Salvin, 1886), stat. rest. is a valid species distinct from *Curvie emesia* (Hewitson, 1867)

Genomic analysis of *Curvie* Grishin, 2019 (type species *Symmachia emesia* Hewitson, 1867) reveals that the genus consists of five species-level taxa (Fig. 11 different colors). *Symmachia yucatanensis* Godman & Salvin, 1886 (type locality in Mexico, Yucatán) is currently treated as a junior subjective synonym of *Curvie emesia* (Hewitson, 1867) (type locality in Nicaragua). However, the two taxa are genetically differentiated at the species level (Fig. 11 purple and blue), i.e., their COI barcodes differ by 2.3% (15 bp). Therefore, we propose that *Curvie yucatanensis* (Godman & Salvin, 1886), **stat. rest.** is a valid species distinct from *Curvie emesia* (Hewitson, 1867). In addition to these two species in the genus *Curvie*, three species do not have available names and are described below as new.

Curvie wing Grishin, new species

http://zoobank.org/AA5E15EB-F2B5-4675-8311-B776FC204789

(Figs. 11 part, 12, 13a)

Definition and diagnosis. This is the northeastern new species of *Curvie* Grishin, 2019 (type species *Symmachia emesia* Hewitson, 1867), distributed in eastern Mexico. It is genetically differentiated from both *Curvie yucatanensis* (Godman & Salvin, 1886), **stat. rest.** (type locality in Mexico, Yucatán) and *Curvie emesia* (Hewitson, 1867) (type locality in Nicaragua) at the species level (Fig. 11 red vs. purple and blue); e.g., their F_{st}/G_{min}/COI barcode difference are 0.37/0.022/2.6% (17 bp) from *C. yucatanensis* and 0.44/0.012/1.8% (12 bp) from *C. emesia*. This new species differs from its relatives by the following

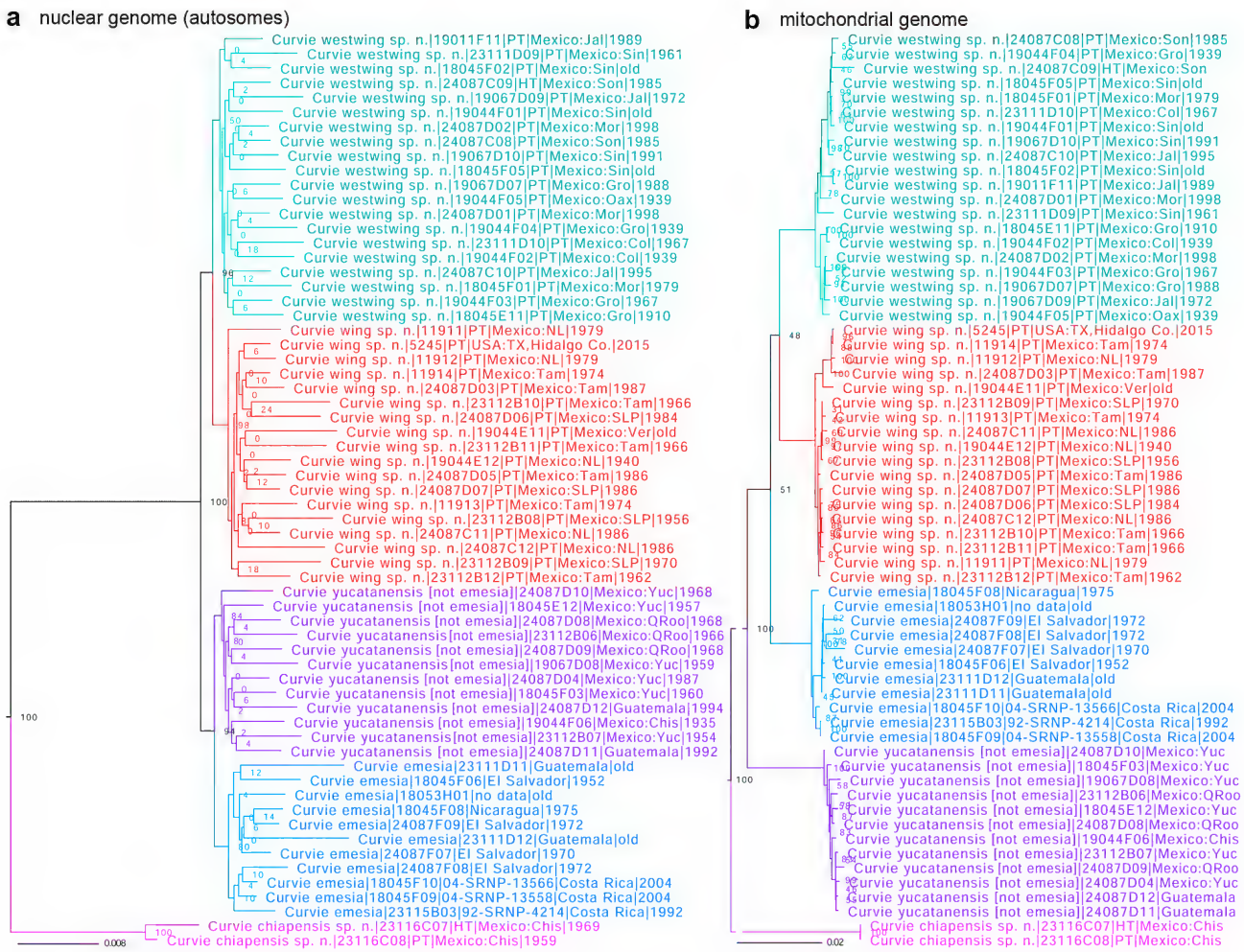


Fig. 11. Phylogenetic trees of *Curvie* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 557,727 positions, and **b)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species are colored differently: *C. westwing* **sp. n.** (cyan), *C. wing* **sp. n.** (red), *C. yucatanensis* (purple), *C. emesia* (blue), and *C. chiapensis* **sp. n.** (magenta).

combination of characters: a comparatively shorter aedeagus; a shorter basal segment of the valva; more curved in ventral view valvae with their distal ends directed posteriad, usually not diverging; and a shorter, bump-like transtilla in lateral view. Due to the cryptic nature of this species and significant individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne312.12.3:A99T, cne312.12.3:A156G, cne312.12.3:T177A, cne312.12.3:G312A, cne312.12.3:A474G; and COI barcode: 88C, T235C, 283T, A472A, C526T.

Barcode sequence of a paratype. Sample NVG-5245, GenBank PV549980, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGAATAGTAGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGAACTTCTGGCTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTTGTACCATTAATATTAGGAGCTCCAGATATAGCATTCCCTCGAA
TAAATAATATAAGATTTTGACTTCTTCCCCCCTCATTATTTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTGTACCCCCCACTTTCTTCTAATATTGC
TCATGGAGGATCATCAGTTGATTTAGCTATTTTTTCATTACATTTAGCTGGGATTTCTTCTATTTTAGGTGCTATTAATTTTATTACTACTATTATTAATATACGAGTAAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCAGTAGGTATTACTGCACTTTTACTTTTATTATCTTTACCCGTATTAGCAGGAGCAATTACTATATTACTAACTGATCGTAATTTAAATACAT
CATTTTTTGACCCAGCAGGAGGAGGAGATCCCATTTTATACCAACACTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 12a, bears the following three printed rectangular labels, two white: [USA: TEXAS: Hidalgo Co. | 2 air mi SE of Relampago | Old Rio Rico Rd., ex larva | GPS: 26.0667°, -97.8837° | larva collected 13-Jun-2015 | on Caesalpinia mexicana, adult ecl. | 4-Jul-2015, Grishin N.V. leg.], [DNA sample ID: | NVG-24103D07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Curvie wing | Grishin].

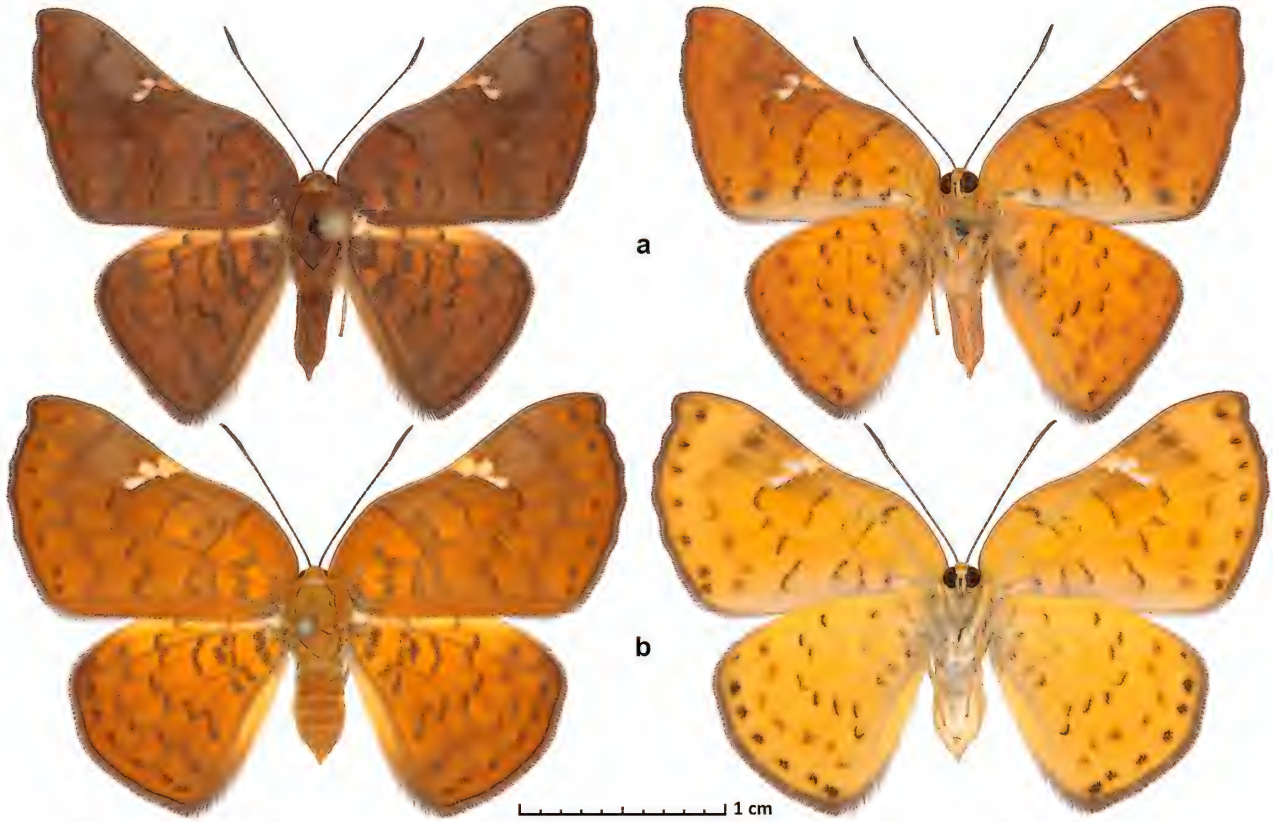


Fig. 12. *Curvie wing* **sp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-24103D07 and **b)** paratype ♀ NVG-24103D08. All *Curvie* specimens (Figs. 12, 14–15) are shown at the same scale to facilitate comparisons.

Fig. 13. Male genitalia of *Curvie* in left lateral (left of the panel letter) and ventral (right of the panel letter) views, data in text or below: **a)** *C. wing* **sp. n.** paratype NVG-23112B10 from Mexico: Tamaulipas (tegumen with uncus and falces detached); **b)** *C. westwing* **sp. n.** paratype NVG-23111D09 from Mexico: Sinaloa; **c)** *C. westwing* **sp. n.** paratype NVG-23111D10 from Mexico: Colima; **d)** *C. yucatanensis* **stat. rest.** NVG-23112B07 Mexico: Yucatán, Chichén Itzá, E. C. Welling leg., genitalia NVG240817-04 [CMNH]; **e)** *C. emesia* NVG-23111D11 Guatemala: Zacapa, genitalia NVG240817-03 [CMNH]; **f)** *C. emesia* NVG-23115B03, 92-SRNP-4214 Costa Rica: Guanacaste Conservation Area, Cuesta Canyon Tigre, 270 m, eclosed 16-Aug-1992, genitalia NVG240817-06 [USNM].

Paratypes: 18♂♂ and 16♀♀ in total: 8♂♂ and 7♀♀ data as the holotype except as stated: 1♂ NVG-3479 30-May, 2♂♂ NVG-3759 and NVG-3762 27-Jun, and ex larvae, found and reared on leaves of *Erythrostemon mexicanus* (Gray 1861) Gagnon & Lewis 2016, eclosed on: 1♀ 11-Jun, 1♂ and 1♀ NVG-24103D08 (Fig. 12b) 12-Jun, 2♀♀ 27-Jun, 1♀ 29-Jun, 1♂ 2-Jul, 1♂ 6-Jul, 1♂ and 1♀ 8-Jul, 1♀ 11-Jul, and 1♂ 13-Jul; USA, Texas, Hidalgo Co., N. V. Grishin leg.: 1♀ Weslaco, 26-Nov-2004 and 1♀ NVG-5245 Los Ebanos, 26.24259, −98.56121, 25-Nov-2015; and Mexico: Tamaulipas: nr. El Abra, Paso del Abra, ex ova on *E. mexicanus*, Roy O. Kendall & C. A. Kendall leg. [TAMU]: 1♂ NVG-11913 15-Feb-1974, genitalia NVG190113-23 and 1♀ NVG-11914 16-Feb-1974, genitalia NVG190113-24; Clench & Miller leg. [CMNH]: 1♂ NVG-23112B11 0-3 mi NW Gomez Farias, 9-Jan-1966 and 1♂ NVG-23112B10 9 mi W Soto la Marina, 8-Jan-1966, genitalia NVG240817-05 (Fig. 13a); and Ciudad Victoria: 1♂ NVG-

23112B12, 16-Aug-1962, H. A. Freeman leg. [CMNH] and Rio San Marcos, John Kemner leg. [MGCL]: 1♂ NVG-24087D03, 1-Jan-1987 and 1♀ NVG-24087D05, 29-Nov-1986; Nuevo Leon: Cola de Caballo: Roy O. Kendall & C. A. Kendall leg., [TAMU]: 1♂ NVG-11911 25-Oct-1979, genitalia NVG190113-21 and 1♀ NVG-11912 23-Oct-1979, genitalia NVG190113-22 and 1♀ NVG-24087C12 19-Jun-1986, I. L. Finkelstein leg. [MGCL]; 1♀ NVG-19044E12, AMNH_IZC 00338007 Hacienda Vista Hermosa, Ville Santiago, 20-Jun-1940, Hoogstraal & Knight leg. [AMNH]; and 1♂ NVG-24087C11 Raices, 8-Jul-1986, John Kemner leg. [MGCL]; San Luis Potosí: Ciudad Valles: H. A. Freeman leg. [CMNH]: 1♂ NVG-23112B08 3-Aug-1956 and 1♀ NVG-23112B09 16-Jul-1970; 1♂ NVG-24087D06 Hwy 70, 22 km W of Ciudad Valles, 17-Oct-1984, H. D. Baggett leg. [MGCL]; and 1♀ NVG-24087D07 Hwy 85, ca. 15 mi S Ciudad Valles, 22-Jun-1986, I. L. Finkelstein leg. [MGCL]; and 1♂ NVG-19044E11, AMNH_IZC 00338006 Veracruz, Jalapa, old [AMNH].

Type locality. USA: Texas, Hidalgo Co., 2 air mi southeast of Relampago, Old Rio Rico Road, GPS 26.0667, −97.8837.

Etymology. The name is inspired by the English name "Curve-winged Metalmark" applied to this species in the U.S. and is treated as a noun in apposition.

Distribution. From South Texas, USA, through eastern Mexico to Veracruz.

Curvie westwing Grishin, new species

http://zoobank.org/B18E8D86-2A4B-46E3-A2E0-05137076A417

(Figs. 11 part, 13b–c, 14)

Definition and diagnosis. This is the northwestern new species of *Curvie* Grishin, 2019 (type species *Symmachia emesia* Hewitson, 1867), distributed in western and southern Mexico. It is sister to the new species described above and is genetically differentiated from it at the species level (Fig. 11 cyan vs. red); e.g., their F_{st}/G_{min}/COI barcode difference are 0.23/0.021/1.7% (11 bp). This new species differs from its relatives by the following combination of characters: a comparatively longer aedeagus; a longer basal segment of the valva; less curved in ventral view, straighter valvae with their distal ends directed posteriad or weakly diverging; and a longer (but still short) transtilla in lateral view. Males of the new species are typically browner (less yellow) beneath, with less distinct markings by the wing margins. Due to the cryptic nature of this species and significant individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne5357.2.5:G18A, cne5357.2.5:T84C, cne5357.2.5:T132C, cne12609.1.3:C102A, cne12609.1.3:T186C; and COI barcode: 88T, T235T, 283T, A472A, C526C.

Barcode sequence of the holotype. Sample NVG-24087C09, GenBank PV549981, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGAATAGTAGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGAACTTCTGGTTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCTATTATAATTGGAGGATTTGGAAATTGACTTGTACCATTAATATTAGGAGCTCCAGATATAGCATTTCCTCGAA
TAAATAATATAAGATTTTGACTTCTTCCCCCCTCATTATTTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTGTACCCCCCACTTTCTTCTAATATTGC
TCATGGAGGATCATCAGTTGATTTAGCCATTTTTTCATTACATTTAGCCGGTATTTCTTCTATTTTAGGTGCTATTAATTTTATTACCACTATTATTAATATACGAGTAAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCAGTAGGTATTACCGCACTTTTACTTTTATTATCTTTACCTGTATTAGCAGGAGCAATTACTATATTATTAACTGATCGTAATTTAAATACAT
CATTTTTTGACCCAGCAGGAGGAGGAGATCCCATTTTATATCAACACTTATTT

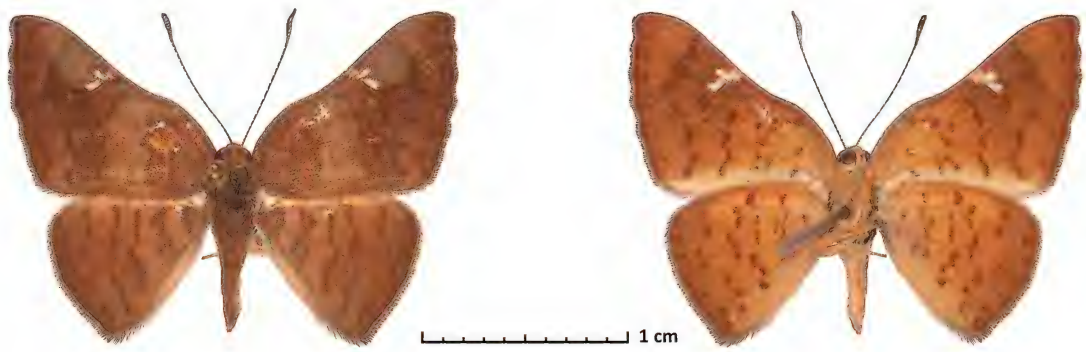


Fig. 14. *Curvie westwing* **sp. n.** holotype ♂ NVG-24087C09 in dorsal (left) and ventral (right) views, data in text.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 14, bears the following four rectangular labels (1st handwritten, others printed), three white: [Rancho El Sabino | 30 m NE of Obregon | Sonora, MEXICO | RAB, 23 Dec 1985], [Bailowitz colln. | MGCL Acc. | 2002-1], [DNA sample ID: | NVG-24087C09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Curvie westwing | Grishin]. The holotype was collected by Richard A. Bailowitz. **Paratypes:** 12♂♂ and 7♀♀ from Mexico: 1♂ NVG-24087C08 Sonora, data as the holotype; Sinaloa: 1♂ NVG-23111D09 48 mi NW of Culiacán, 23-Oct-1961, genitalia NVG240817-01 (Fig. 13b) [CMNH]; 1♀ NVG-19067D10 Hwy 40, mile 286, 26-27-Dec-1991, R. Wells [UCDC]; 1♂ NVG-19044F01, AMNH_IZC 00338008 Mazatlan, old [AMNH]; and Venadio, old [USNM]: 1♂ NVG-18045F02, USNMENT 01466474 Wm. Schaus collection and 1♀ NVG-18045F05, USNMENT 01466477 donated by B. P. Clark; Jalisco: 1♂ NVG-24087C10 dirt Rd. 15.5 km S of Mismaloya, hotel on Rte. 200, 13-15-Nov-1995, B. O'Hara collection [MGCL]; 1♂ NVG-19011F11 Hwy 200 below Vallarta, Las Juntas Verano, 1000 m, 8-Aug-1989, J. Kemner leg. [TMMC]; and 1♀ NVG-19067D09 Hwy 79, 1–3 mi NE of El Grullo Jnct, 4600', 28-Dec-1972, R. Wells leg. [UCDC]; Colima: 1♂ NVG-23111D10 Comala, 2100 ft, 22-May-1967, R. G. Wind leg, genitalia NVG240817-02 (Fig. 13c) [CMNH] and 1♀ NVG-19044F02, AMNH_IZC 00338009 Santiago Bay, 25-Nov-1939, F. H. Rindge collection [AMNH]; Morelos: 1♂ NVG-18045F01, USNMENT 01466473 no location details, Aug-1979, Phil Mays leg. [USNM] and 2♂♂ NVG-24087D01 and NVG-24087D02 Cuernavaca, Feb-1998, J. Brenner coll. [MGCL]; Guerrero:1♂ NVG-19044F03, AMNH_IZC 00338010 1.5 mi W of Acapulco, 60 m, 4-Sep-1967, Miller & Pine leg. [AMNH]; 1♀ NVG-19067D07 Acapulco, 22-Mar-1988 [UCDC]; 1♀ NVG-19044F04, AMNH_IZC 00338011 Papanoa, 1-Dec-1939, F. H. Rindge collection [AMNH]; and 1♂ NVG-18045E11, USNMENT 01466471 Sierra de Guerrero, Dec-1910, R. Muller [USNM]; and 1♀ NVG-19044F05, AMNH_IZC 00338012 Oaxaca, Santa Cruz Bay, 3-Dec-1939, F. H. Rindge collection [AMNH].

Type locality. Mexico: Sonora, 30 mi northeast of Ciudad Obregón, Rancho El Sabino.

Etymology. The name indicates a more western distribution of this sister to *C. wing* **sp. n**. and is treated as a noun in apposition.

Distribution. Western and southern Mexico, from Sonora to Oaxaca.

Curvie chiapensis Grishin, new species

http://zoobank.org/99F3F7E6-AB3D-4C04-AD4E-A44E87FCA079

(Figs. 11 part, 15)

Definition and diagnosis. This new species from Chiapas, Mexico, is sister to all other species of *Curvie* Grishin, 2019 (type species *Symmachia emesia* Hewitson, 1867) and is more strongly differentiated genetically from them (Fig. 11 magenta vs. others), e.g., COI barcodes differ between the new species and a specimen of *Curvie yucatanensis* (Godman & Salvin, 1886), **stat. rest.** (type locality in Mexico, Yucatán) from Chiapas by 6.4% (42 bp). The new species differs from its relatives by more angular wings with a more strongly hooked forewing apex; only two, not three, pale spots by the forewing costa in males, which also have a rustier, redder, and darker ventral side of the wings with a less defined dark pattern; a darker, grayer, less saturated color of the dorsal side of the wings in females, which in addition have a wider pale patch by the forewing costa, more weakly separated into three spots; and a more contrasting paler (rusty) apical spot on the forewing. Due to unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne10339.2.10:A99T, cne10339.2.10:A114C, cne3135.7.1:T1353C, cne3135.7.1:G1362A, cne2156.9.4:A84T; and COI barcode: T103C, A202G, T238C, T487C, T574A.

Barcode sequence of the holotype. Sample NVG-23116C07, GenBank PV549982, 658 base pairs:

AACATTATATTTTATTTTTGGTATTTGAGCAGGAATAGTAGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGAACTTCAGGTTCTTTAATTGGAGACGATCAAATTTATAATACT
ATTGTAACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGATTAGTGCCATTAATATTAGGGGCCCCAGATATAGCTTTCCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCTTTATTTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTGTACCCCCCACTTTCTTCTAATATCGC
TCATGGAGGATCATCAGTTGATTTAGCTATTTTTTCCTTACATTTAGCTGGAATTTCTTCTATTTTAGGAGCAATTAATTTTATTACCACTATTATTAATATACGTATTAATAATTTATCT
TTCGATCAAATACCTTTATTTATTTGATCAGTAGGTATTACCGCTCTTTTACTTTTATTATCTTTACCTGTTTTAGCGGGTGCTATTACAATATTATTAACTGATCGTAATCTTAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

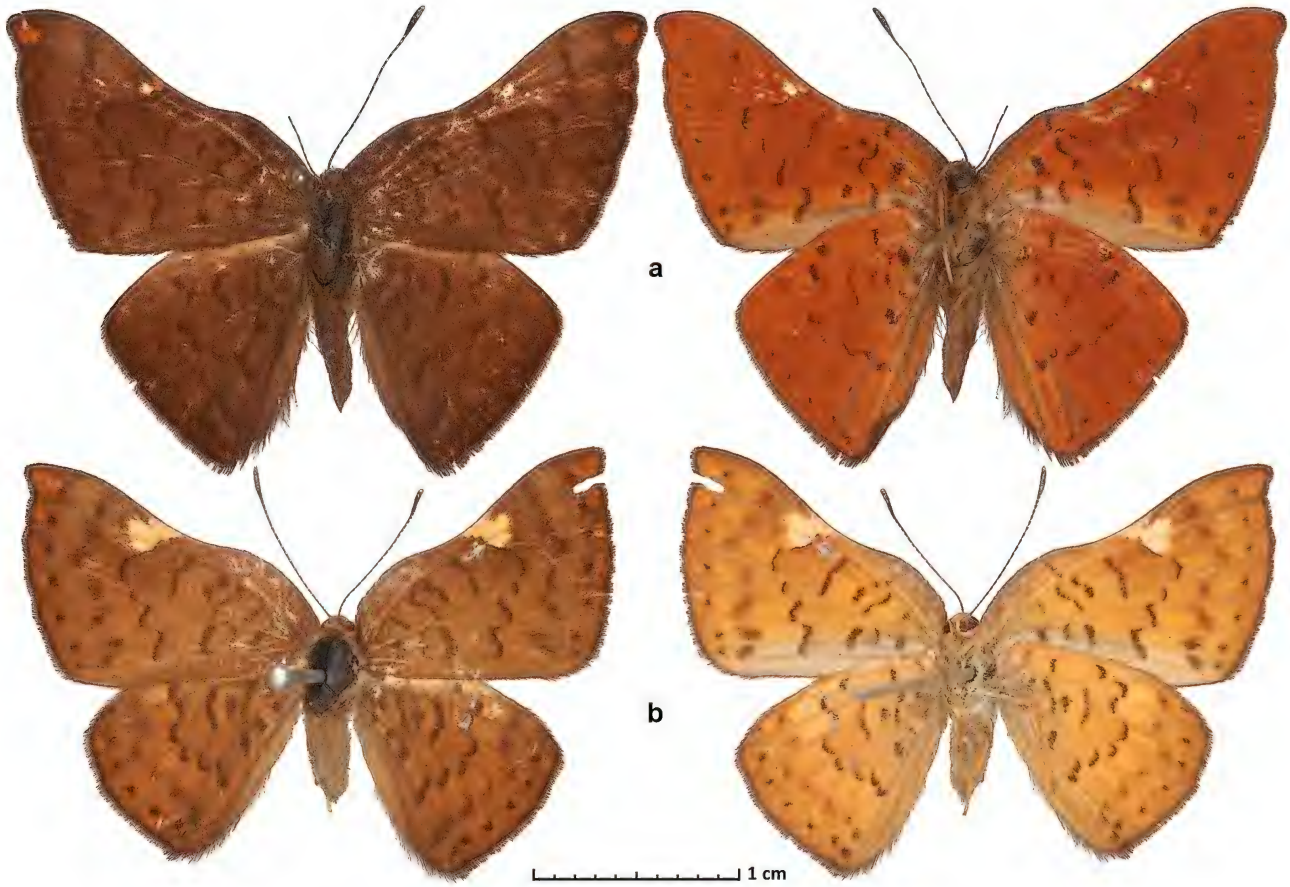


Fig. 15. *Curvie chiapensis* **sp. n.** in dorsal (left) and ventral (right) views, data in text.
a) holotype ♂ NVG-23116C07 and **b)** paratype ♀ NVG-23116C08.

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 15a, bears the following four printed (text in italics handwritten) rectangular labels, three white: [T. Escalante | *Las Delicias* | *Chis-VII-69*], [A. C. Allyn | Acc. 1973–48], [DNA sample ID: | NVG-23116C07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Curvie chiapensis | Grishin]. **Paratype:** 1♀ NVG-23116C08 Mexico, Chiapas, Santa Rosa Comitán, Apr-1959, T. Escalante leg. [USNM] (Fig. 15b).

Type locality. Mexico: Chiapas, Las Delicias.

Etymology. The name is given for the type locality and is an adjective.

Distribution. Currently known only from Chiapas in Mexico.

Emesis (*Tenedia*) *tinia* Grishin, new species

http://zoobank.org/D9E4D5FA-6B75-48AB-972E-9A232C625376

(Figs. 16 part, 17)

Definition and diagnosis. A specimen of *Emesis* [Fabricius], 1807 (type species *Hesperia ovidius* Fabricius, 1793, a junior subjective synonym of *Papilio cereus* Linnaeus, 1767) from Argentina belongs to a lineage originating in deep radiation of the subgenus *Tenedia* Grishin, 2019 (type species *Emesis tenedia* C. Felder & R. Felder, 1861) thus being sister to several distant relatives, such as *Emesis ocypore* (Geyer, 1837) (type locality given as "Africa", likely in the Amazonian region) and *Emesis angularis* Hewitson, 1870 (type locality in Ecuador) (Fig. 16), and, therefore, it represents a new species. This species is not particularly similar to any other *Emesis* and might have been identified as *Emesis diogenia* Prittwitz, 1865 (type locality in Brazil: Rio de Janeiro) due to locality and some similarity in wing shape,

but it lacks two prominent submarginal spots (near the apex and tornus) of *E. diogenia* on the ventral hindwing. The new species differs from its relatives by smaller size, narrower wings, dull brown coloration with alternating darker brown and caramel brown bands and patches outlined by darker lines, dashes, and lunules; more uniformly colored on the ventral side with a pattern of rather evenly distributed spots and dashes and a more prominent discal darker band as the basal outline of the dark-brown streaks forming a broken wavy line. Due to unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne4719.2.2:T30C, cne3798.9.9:G51A, cne1556.1.19:C72T, cne4207.2.2:C160T, cne1820.1.2:T180C, cne3116.1.3:C69C (not T); and COI barcode: A40G, T83C, A202C, C235T, T283C, T520C, T547C.

Barcode sequence of the holotype. Sample NVG-24032C07, GenBank PV549983, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGGGCAGGAATAGTGGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCTATTATAATTGGAGGATTTGGTAATTGATTAGTCCCATTAATATTAGGAGCTCCAGACATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCCCTCATTAATCTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACAGTGTACCCCCCACTTTCATCTAATATCGC
CCATGGTGGATCATCAGTGGATTTAGCCATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCAATTAATTTTATCACCACTATTATCAATATACGAATTAATAATTTATCA
TTTGATCAAATACCTCTTTTTGTCTGATCTGTAGGCATTACAGCACTTTTACTTTTATTATCCTTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGACCCTGCGGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 17, bears the following five rectangular labels (1st handwritten, others printed), four white: [Argentinia | Rschus.], [Coll. | Staudinger], [DNA sample ID: | NVG-24032C07 | c/o Nick V. Grishin], [{QR Code} MfN URI | http://coll.mfn- | berlin.de/u/ | 09c87b], and one red [HOLOTYPE ♂ | Emesis (Tenedia) | tinia Grishin].

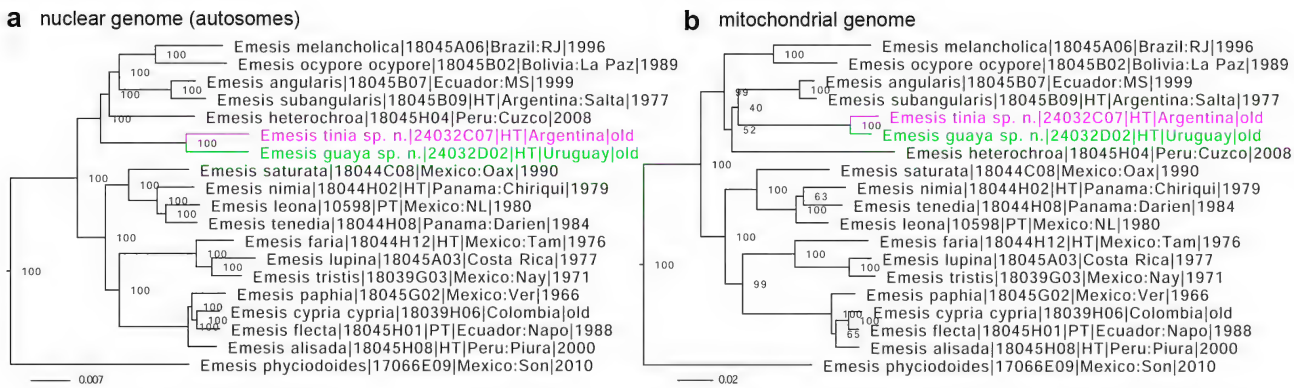


Fig. 16. Phylogenetic trees of *Emesis* (*Tenedia*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 7,184,877 positions, and **b)** the mitochondrial genome, showing the phylogenetic position of *E. tinia* **sp. n.** (magenta) and *E. guaya* **sp. n.** (green). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

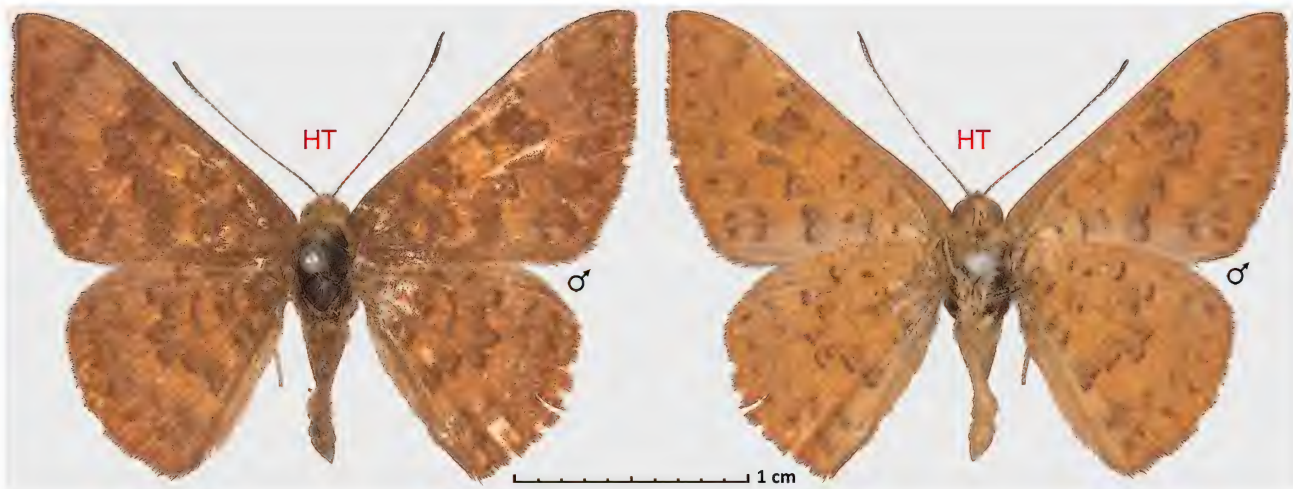


Fig. 17. *Emesis* (*Tenedia*) *tinia* **sp. n.** holotype ♂ NVG-24032C07 in dorsal (left) and ventral (right) views, data in text.

Type locality. Argentina.

Etymology. The name is given for the country with the type locality: [Argen]*tin{i}a*, and also hints at a small size of this species. The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in Argentina.

Emesis (*Tenedia*) *guaya* Grishin, new species

http://zoobank.org/DC681E0D-9AFE-4559-9B1E-B9725FD12AC0

(Figs. 16 part, 18)

Definition and diagnosis. A specimen from Uruguay is sister to *Emesis* (*Tenedia*) *tinia* **sp. n.** (type locality in Argentina) described above, but is genetically differentiated from it at the species level (Fig. 16); e.g., their COI barcodes differ by 2.1% (14 bp), which in the presence of phenotypic differences suggests that it belongs to a new species. This new species is most similar to *E. tinia* **sp. n.** in is smaller size and wing pattern consisting of darker wavy lines, spots, and dashes but differs from it by slightly broader wings, a weaker contrast between darker brown and paler brown areas on the dorsal side of the wings, a more prominent postdiscal dark-brown wavy line on the ventral forewing consisting of closer connected elements in every cell, and a not as strongly developed darker discal band basad of this wavy line as in *E. tinia* **sp. n**. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne977.2.4:A87G, cne977.2.4:T99C, cne2582.13.11:A75G, cne5556.4.1:C600T, cne5556.4.1:G606A; and COI barcode: A31C, A40G, A202C, T478A, T520C, T547C.

Barcode sequence of the holotype. Sample NVG-24032D02, GenBank PV549984, 658 base pairs:

AACATTATATTTTATTTTTGGAATTTGAGCCGGAATAGTGGGAACATCTTTAAGTTTATTAATTCGAATAGAATTAGGAACTTCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATGGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTCCCATTAATATTAGGAGCTCCAGACATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGATTATTACCCCCCTCATTAATTTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACAGTGTACCCCCCACTTTCATCTAATATCGC
CCATGGAGGATCATCAGTAGATTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCAATTAATTTTATCACCACTATTATCAATATACGAATTAATAAATTATCA
TTTGATCAAATACCTCTTTTTTGTCTGATCTGTAGGCATTACAGCACTTTTACTTTTATTATCCTTACCTGTTTTAGCGGGAGCTATTACTATATTATTAACTGATCGTAATTTAAACACAT
CATTTTTTGATCCTGCAGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 18, bears the following five rectangular labels (1st handwritten, others printed), four white: [Uruguay | Rschus.], [Coll. | Staudinger], [DNA sample ID: | NVG-24032D02 | c/o Nick V. Grishin], [{QR Code} MfN URI | http://coll.mfn- | berlin.de/u/ | 0a0d27], and one red [HOLOTYPE ♂ | Emesis (Tenedia) | guaya Grishin].

Type locality. Uruguay.

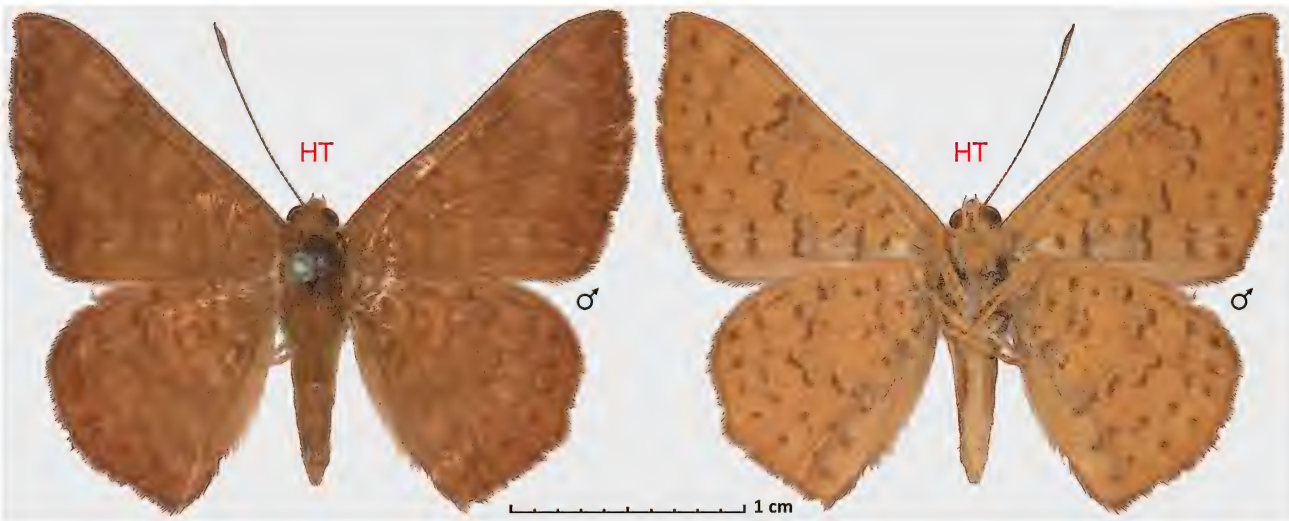


Fig. 18. *Emesis* (*Tenedia*) *guaya* **sp. n.** holotype ♂ NVG-24032D02 in dorsal (left) and ventral (right) views, data in text.

Etymology. The name is given for the country with the type locality: [Uru]*guay* + *a*, and also refers to a prominently defined wire-like meandering discal dark line on the ventral forewing (in Spanish, guaya may mean cable or wire). The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in Uruguay.

Emesis (*Aphacitis*) *bugaba* Grishin, new species

http://zoobank.org/1A2FE025-11D5-4167-A28C-39E8452FE405

(Figs. 19 part, 20)

Definition and diagnosis. Genomic analysis of a pair of specimens from Bugaba, Panama, places them in a nuclear genome clade sister to several species of the subgenus *Aphacitis* Hübner, [1819] (type species *Papilio dyndima* Cramer, [1780], a junior homonym, current name applied to this species is *Papilio lucinda* Cramer, [1775]), such as *Emesis aurimna* (Boisduval, 1870) (type locality in Colombia) and *Emesis parvissima* Kaye, 1921 (type locality in Trinidad) (Fig. 19a), and, therefore, this pair represents a new species. In the mitochondrial genome tree, this new species is closest to another Panamanian species, *Emesis auripana* Grishin, 2024 (Fig. 19b), likely due to mitochondrial introgression. This new species differs from its relatives by males without a prominent but small pale spot near the forewing apex above (present in *E. aurimna*); with a developed apical pale frosting on the dorsal forewing (absent in *E. parvissima*), scattered over a wider area and more weakly separated from the rest of the wing by a paler band than in *E. auripana* and *Emesis aurichica* Grishin, 2024 (type locality in Mexico: Chiapas), but less distinct than in *Emesis pruinapicalis* Grishin, 2024 (type locality in Panama: Darien); being redder (rather than yellower) on the ventral side with more diffuse at the margins postdiscal brown bands; and females with a well-developed subapical cream patch and an apical triangle (larger than in *E. aurichica*), a paler submarginal smudge in the forewing cell M_2-M_3, and a stronger developed brown pattern on the beige ventral side. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: cne2443.2.1:A909G, cne2443.2.1:C912T, cne3195.1.6:A465G, cne243.2.8:A111G, cne5807.10.4:G303A; and COI barcode: A302G, C376T, 508C, T610C, A625A.

Barcode sequence of the holotype. Sample NVG-18053H09, GenBank PV549985, 658 base pairs:

AACATTATACTTTATTTTTGGAATTTGATCAGGAATAGTCGGCACATCTTTAAGTTTATTAATTCGAATAGAATTAGGAACCTCAGGCTCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAACTGATTAGTTCCATTAATATTAGGAGCACCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCGCCATCATTAATTTTATTAATTTCAAGAAGAGTTGTAGAAAATGGAGCAGGAACAGGATGAACAGTGTACCCCCCACTTTCATCTAATATTGC
CCATGGAGGAGCTTCAGTTGATTTAGCTATTTTTTCCCTTCATTTAGCTGGTATTTCATCTATTTTAGGAGCAATTAATTTTATCACAACAATCATTAATATACGTATTAATAATATGTCA
TTTGATCAAATACCATTATTTGTCTGATCTGTTGGAATTACAGCTCTTTTACTTTTATTATCTCTTCCAGTTTTAGCCGGAGCTATTACTATATTATTAACAGATCGTAATTTAAATACAT
CTTTCTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 20a, bears the following five rectangular labels (3rd handwritten and framed, others

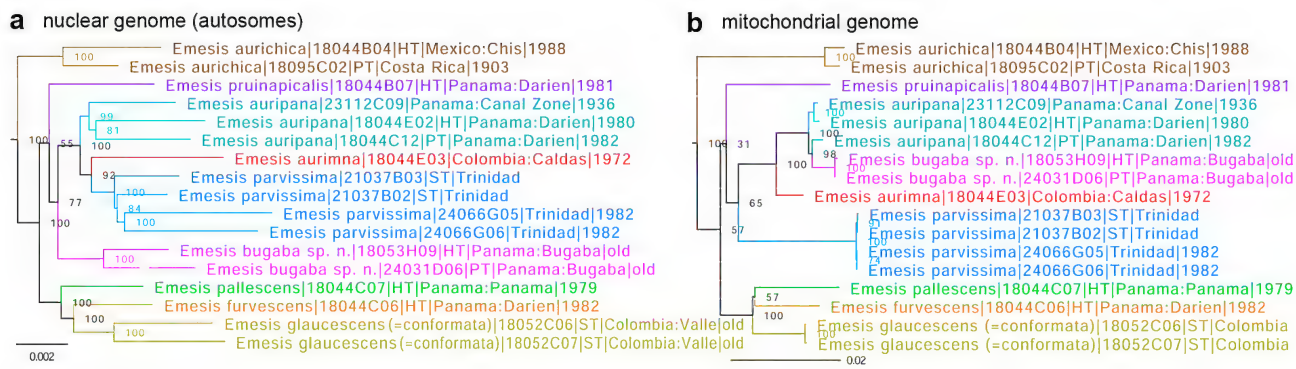


Fig. 19. Phylogenetic trees of selected *Emesis* (*Aphacitis*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,086,919 positions, and **b)** the mitochondrial genome. Different species are colored differently: *E. aurichica* (brown), *E. pruinapicalis* (purple), *E. auripana* (cyan), *E. aurimna* (red), *E. parvissima* (blue), *E. bugaba* **sp. n.** (magenta), *E. pallescens* Grishin, 2024 (green), *E. furvescens* Grishin, 2024 (orange), and *E. glaucescens* Talbot, 1929 (olive). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. A gap in a branch indicates that a segment of the branch was cut out to reduce its length (to allow an increase in the font size).

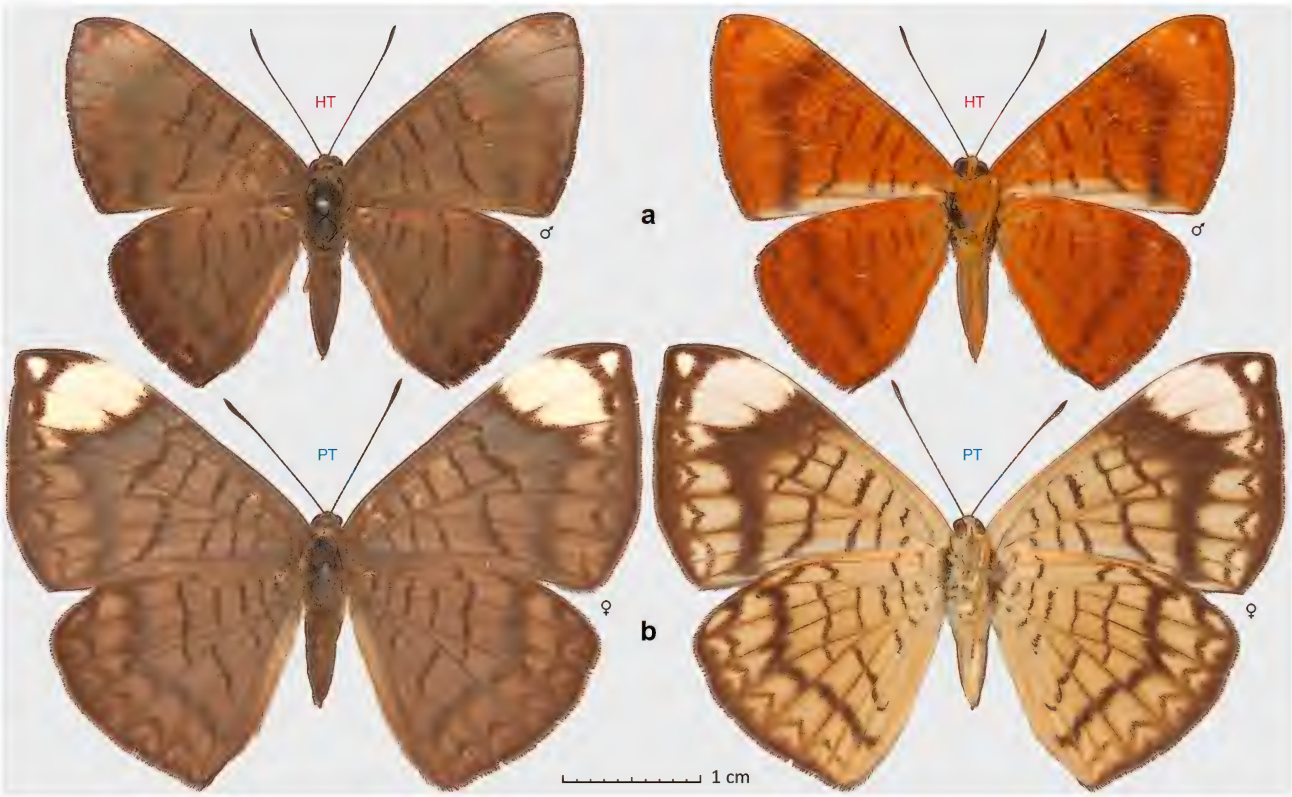


Fig. 20. *Emesis* (*Aphacitis*) *bugaba* **sp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-18053H09 and **b)** paratype ♀ NVG-24031D06.

printed; 3rd green, 5th red, and others white): [Panama | Bugaba | e.c.H.Stichel], [3268], [aurimna Bsd.], [DNA sample ID: | NVG-18053H09 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Emesis (Aphacitis) | bugaba Grishin]. The 2nd label gives the specimen number in the Stichel collection. **Paratype:** 1♀ NVG-24031D06 the same data as the holotype but Stichel collection number 3271 (Fig. 20b).

Type locality. Panama: Chiriquí Province, Bugaba.

Etymology. The name is given for the type locality and is a noun in apposition.

Distribution. Currently known only from western Panama.

Synargis rectanga Grishin, new species

http://zoobank.org/00AE0604-72AE-4E6D-B0DD-663BCC892274

(Figs. 21 part, 22a)

Definition and diagnosis. A female from the Andes of northern Peru (Fig. 22a) is sister to *Synargis maxidifa* Grishin, 2024 (type locality Peru: Loreto Region, Pumayacú) (Fig. 22b), a lowland species, but is genetically differentiated from it (Fig. 21); e.g., their COI barcodes differ by 1.5% (10 bp), and, therefore, represents a new species. This new species differs from its relatives by the following combination of characters: a broad (3–4 times broader than submarginal cream patches and bands) and rather rectangular in shape cream diagonal band through both wings from the end of the forewing discal cell to the inner margin of the hindwing; pale-yellow, cream-colored spots and bands; prominently checkered fringes; somewhat sinuous outer margins of both wings; diffuse and irregular edges of pale submarginal patches and bands; and prominent cream spots crossing the brown border of the ventral side of the wings. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the

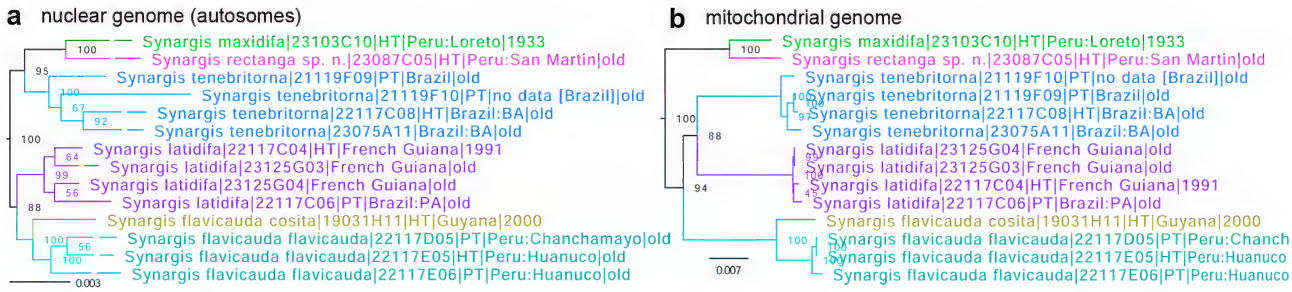


Fig. 21. Phylogenetic trees of selected *Synargis* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 345,000 positions, and **b)** the mitochondrial genome. Different species are colored differently: *S. maxidifa* (green), *S. rectanga* **sp. n.** (magenta), *S. tenebritorna* Grishin, 2024 (blue), *S. latidifa* Grishin, 2024 (purple), and *S. flavicauda* Grishin, 2024 (cyan with *S. flavicauda cosita* Grishin, 2024 in olive). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Gaps in terminal branches indicate that a segment of a branch was cut out to reduce its length (to allow an increase in the font size), i.e., a branch with a gap is longer than shown.

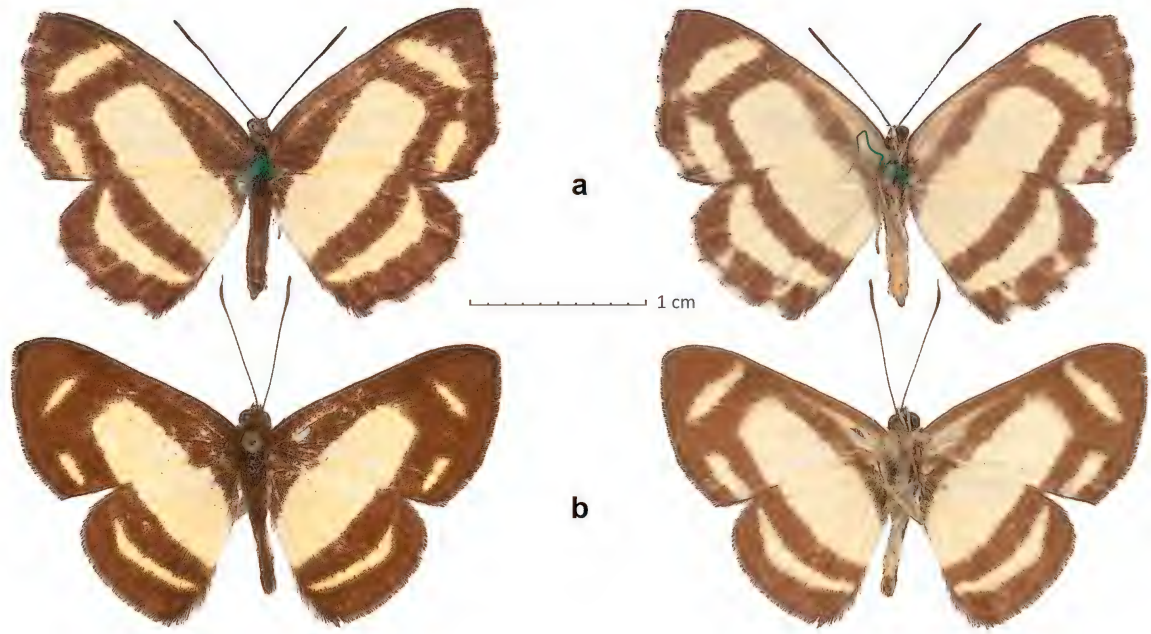


Fig. 22. *Synargis* specimens in dorsal (left) and ventral (right) views, data in text:
a) *S. rectanga* **sp. n.** holotype ♀ NVG-23087C05 and **b)** *S. maxidifa* Grishin, 2024 holotype ♂ NVG-23103C10.

nuclear genome: cne3016.1.2:A390G, cne3016.1.2:G402T, cne12689.1.1:G111A, cne457.6.18:G125C, cne2264.8.5:A189G; and COI barcode: T59A, G125A, T169C, T358C, A494T.

Barcode sequence of the holotype. Sample NVG-23087C05, GenBank PV549986, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGTATAATAGGAACATCTCTTAGTTTAATAATTCGAATAGAATTAGGAACTCCTGAATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTATTACAGCTCATGCATTTATTATAATATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCTCCAGATATAGCTTTCCCCCGTA
TAAATAACATAAGATTTTGATTATTACCTCCTTCTTTATTTTTATTAATCTCCAGAAGAATTGTTGAAAATGGTGCAGGAACTGGATGAACAGTGTACCCCCCACTTTCATCAAACATTGC
TCATAGAGGAACTTCTGTTGATTTAGCCATTTTTTCTCTTCATTTAGCTGGAATTTCTTCAATCTTAGGTGCAATTAACTTTATTACTACTATTATTAATATACGTATTAATAATTTATCA
TTTGATCAATTACCTTTATTTATTTGATCAGTAGGAATTACTGCTCTTCTTCTTTTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAATTTAAATACAT
CTTTTTTTGATCCTGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♀ deposited in the Zoologische Staatssammlung München, Germany (ZSMC), illustrated in Fig. 22a, bears the following four rectangular labels (2nd handwritten, others printed), three white: [Tarap. | Perú], [♀Nymph. regulus F. | Peru *], [DNA sample ID: | NVG-23087C05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Synargis | rectanga Grishin].

Type locality. Peru: San Martin Region, Tarapoto.

Etymology. The name is given for the rectangular shape of a wide cream-colored discal band and its brown frame, and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in the lower eastern Andes of Northern Peru.

Lucispila Grishin, new subgenus

http://zoobank.org/EB3A4B74-169A-4427-BE00-7ADA53A264E3

Type species. *Hesperia lucianus* Fabricius, 1793.

Definition. Genomic analysis reveals that *Parvospila* J. Hall, 2018 (type species *Papilio emylius* Cramer, 1775) partitions into two prominent clades genetically differentiated at least at the subgenus level (Fig. 23); e.g., their COI barcodes may differ by as much as 12.1% (80 bp). One of the clades includes the type species of *Parvospila*, and the other corresponds to a new genus group taxon that is conservatively proposed at the subspecies level. This new subgenus encompasses the *lucianus* group of Hall (2018), and the phenotypic characters and the description referring to this species group given by Hall apply to this subgenus. In brief, this new subgenus differs from its relatives by a combination of the following characters: absent submarginal white spots on the dorsal side of the wings, even near the apex; a more projecting distad ventral corner of the uncus in lateral view, a longer (but still short) saccus; narrower and upturned at the narrowing tip valvae; and a longer aedeagus with a cluster of much longer and prominent spines in vesica. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cne2651.14.17:A660G, cne2651.14.17:C677A, cne96.1.3:G91C, cne96.1.3:T108C, cne4571.6.1:A472C; and in COI barcode: T169A, A469T, T482G, C538A, A643T.

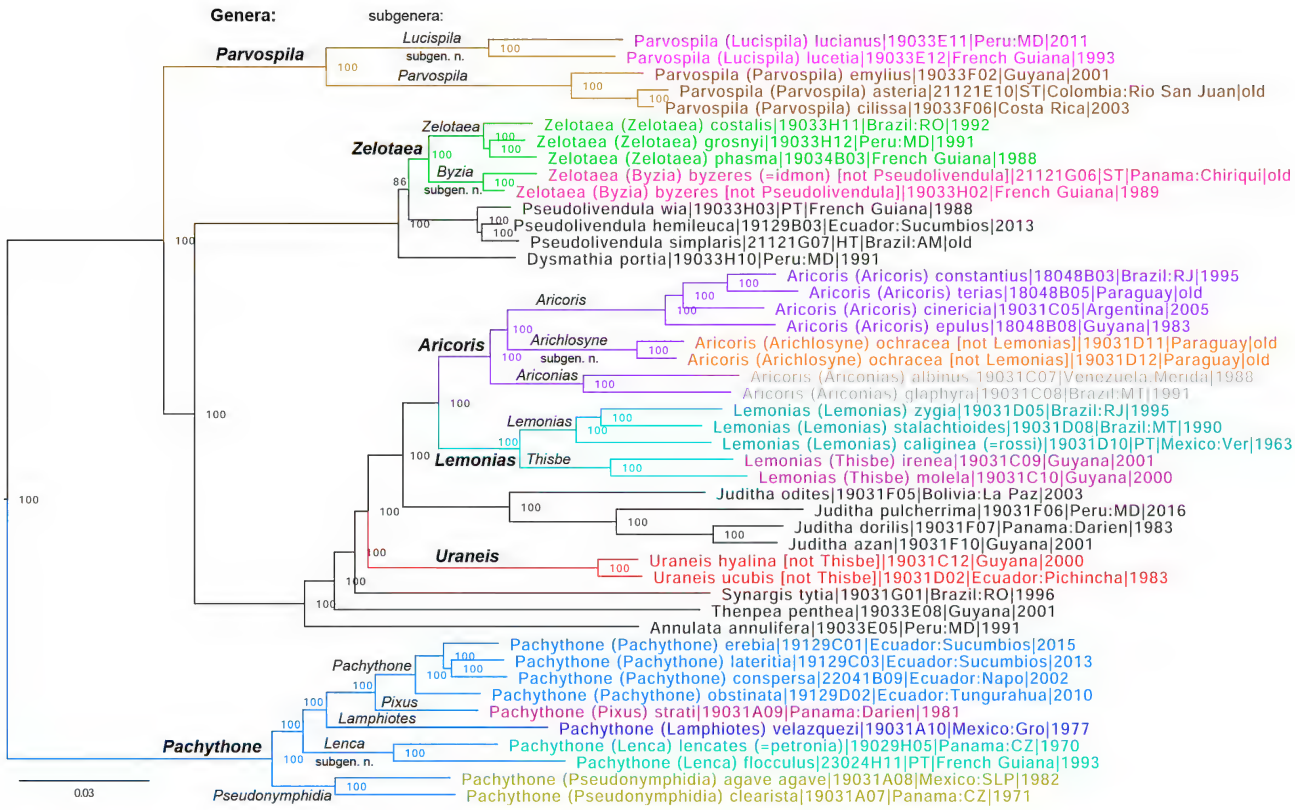


Fig. 23. Phylogenetic trees of selected *Nymphidiini* constructed from protein-coding regions in the nuclear genome (autosomes), based on 4,956,768 positions. Different genera are colored differently, and different subgenera are labeled in different colors: *Parvospila* (brown with subgenus *Lucispila* **subgen. n.** labeled in magenta), *Zelotaea* (green with subgenus *Byzia* **subgen. n.** labeled in pink), *Aricoris* (purple with subgenera *Arichlosyne* **subgen. n.** and *Ariconias* **stat. nov.** labeled in orange and gray, respectively), *Lemonias* (cyan with subgenus *Thisbe* **stat. nov.** labeled in bright purple), *Uraneis* **stat. nov.** (red), and *Pachythone* (blue with subgenera *Pixus* Callaghan, 1982, *Lamphiotes* Callaghan, 1982, *Lenca* **subgen. n.**, and *Pseudonymphidia* **stat. nov.** labeled in maroon, dark blue, aquamarine, and olive, respectively). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

Etymology. The name is a fusion of the type species and genus names: *luci*[anus] + [Parvo]*spila*. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Hesperia lucianus* Fabricius, 1793) and *Echenais lucetia* Hübner, 1821.

Parent taxon. Genus *Parvospila* J. Hall, 2018.

Byzia Grishin, new subgenus

http://zoobank.org/858E778D-D277-4FD6-98C9-580C0A8B4C9A

Type species. *Lemonias byzeres* Hewitson, 1872.

Definition. Nuclear genome phylogeny reveals that *Lemonias byzeres* Hewitson, 1872 (type locality in Brazil: Pará) currently placed in the genus *Pseudolivendula* J. Hall, 2018 (type species *Lemonias hemileuca* Bates, 1868) is not monophyletic with its type species and instead is a confidently supported sister to *Zelotaea* H. Bates, 1868 (type species *Zelotaea phasma* Bates, 1868), genetically differentiated from *Z. phasma* at least at the subgenus level (Fig. 23); e.g., their COI barcodes differ by 10.6% (70 bp). To restore monophyly and not willing to erect a new genus for *L. byzeres* and *Nymphidium candace* H. Druce, 1904 (type locality in Brazil: Rio de Janeiro), we transfer them to the genus *Zelotaea* as *Zelotaea byzeres* (Hewitson, 1872) **comb. nov.** and *Zelotaea candace* (H. Druce, 1904) **comb. nov**. The distinct lineage with *Z. byzeres* corresponds to a new genus group taxon that is conservatively proposed as a subgenus. This new subgenus encompasses the *byzeres* group of Hall (2018), and the phenotypic characters and the description referring to this species group given by Hall apply to this subgenus. In brief, this new subgenus differs from its relatives by a combination of the following characters: no white patch in the tornal half of the hindwing; a rufous-brown tone of dorsal wings in males; a more rectangular than triangular uncus in lateral view; a mostly straight to slightly concave dorsal margin of the valva; a narrowing to a sharp and slightly upturned point valva in lateral view; and fused cornuti. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cne7747.1.11:A78T, cne5623.1.1:C240T, cne2099.4.1:A2067G, cne23345.2.2:C136T, cne1842.8.1:T304C; and in COI barcode: A44T, 220A, T460C, A508T, A637T.

Etymology. The name is formed from the type species name and is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Lemonias byzeres* Hewitson, 1872) and *Nymphidium candace* H. Druce, 1904.

Parent taxon. Genus *Zelotaea* H. Bates, 1868.

Arichlosyne Grishin, new subgenus

http://zoobank.org/039B5F09-E16D-4BA1-8243-689F19CA0085

Type species. *Apodemia ochracea* Mengel, 1902.

Definition. Nuclear genome phylogeny reveals that *Apodemia ochracea* Mengel, 1902 (type locality in Paraguay), currently in the genus *Lemonias* Hübner, [1807] (type species *Lemonias zygia* Hübner, 1807), is not monophyletic with it and instead is sister to *Aricoris* Westwood, 1851 (type species *Aricoris tisiphone* Westwood, 1851, which is a junior subjective synonym of *Erycina tutana* Godart, [1824]), being genetically differentiated from it at the subgenus level (Fig. 23 purple and labeled orange); e.g., their COI barcodes differ by 9% (59 bp). Therefore, we transfer *Apodemia ochracea* and phenotypically similar to it *Riodina*? *theodora* Godman, 1903, and *Riodina*? *albofasciata* Godman, 1903 from *Lemonias* to *Aricoris* forming *Aricoris ochracea* (Mengel, 1902), **comb. nov.**, *Aricoris theodora* (Godman, 1903), **comb. nov.**, and *Aricoris albofasciata* (Godman, 1903), **comb. nov**. Because the lineage with *Aricoris ochracea* does not contain type species of any available genus group names, it represents a new subgenus.

This new subgenus differs from its relatives by the following combination of characters (see Hall and Harvey (2001) for illustrations and discussion): long falces, not shorter than the tegumen with the uncus; a uniformly broad uncus, not narrowing terminally in dorsal view and with a concave distal margin; a single spike-shaped cornutus in the vesica; the eights abdomen sternite in males is approximately rectangular, not narrowing terminally; the ductus bursae is compressed laterally towards the ostium bursae; the forewing costal margin in males is rather straight to slightly concave in the middle, and the outer margin is concave near the tornus; and wings are dark brown with orange and white bands, patches, and spots (one white spot is in the forewing discal cell). In DNA, a combination of the following characters is diagnostic in the nuclear genome: cne1364.1.2:A279G, cne1364.1.2:G296A, cne13787.2.1:T70C, cne13787. 2.1:A84G, cne2068.2.1:A4182G; and in COI barcode: A73G, 139C, T304C, T532A, A541T.

Etymology. This *Aricoris* is somewhat similar in wing patterns to some species of *Chlosyne* Butler, 1870 (Nymphalidae): *Ari*[coris] + *Chlosyne*. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Apodemia ochracea* Mengel, 1902), *Riodina*? *albofasciata* Godman, 1903, and *Riodina*? *theodora* Godman, 1903.

Parent taxon. Genus *Aricoris* Westwood, 1851.

Ariconias J. Hall & Harvey, 2002 is a subgenus of *Aricoris* Westwood, 1851

Currently treated as a genus, *Ariconias* J. Hall & Harvey, 2002 (type species *Lemonias albinus* C. Felder & R. Felder, 1861) is phenotypically similar (especially in wing shape) to the subgenus *Arichlosyne* **subgen. n.** (type species *Apodemia ochracea* Mengel, 1902) of *Aricoris* Westwood, 1851 (type species *Aricoris tisiphone* Westwood, 1851, which is a junior subjective synonym of *Erycina tutana* Godart, [1824]), and these genus group taxa are differentiated genetically from each other at the subgenus level (Fig. 23 purple); e.g., their COI barcodes differ by 8.5% (56 bp) (*Ariconias* and *Aricoris*) and 8.7% (57 bp) (*Ariconias* and *Arichlosyne*). Therefore, we propose that *Ariconias* J. Hall & Harvey, 2002 **stat. nov.** is a subgenus of *Aricoris* Westwood, 1851.

Thisbe Hübner, [1819] is a subgenus of *Lemonias* Hübner, [1807]

Currently treated as a genus, *Thisbe* Hübner, 1819 (type species *Papilio belise* Stoll, 1782, which is a junior subjective synonym of *Papilio irenea* Stoll, 1780) is genetically differentiated from *Lemonias* Hübner, [1807] (type species *Lemonias zygia* Hübner, 1807) at the subgenus level (Fig. 23 cyan); e.g., their COI barcodes differ by 8.4% (55 bp). Therefore, we propose that *Thisbe* Hübner, 1819 **stat. nov.** is a subgenus of *Lemonias* Hübner, [1807]. Moreover, we find that *Thisbe*, as currently circumscribed, is not monophyletic (Fig. 23 red and cyan labeled in bright purple), and some species included in *Thisbe* belong to distinct genera, as elaborated upon in the next section.

Uraneis Bates, 1868 is a valid genus and *Esthemopheles* Röber, 1903 is its junior subjective synonym

Currently included within *Thisbe* Hübner, [1819] (type species *Papilio belise* Stoll, 1782, which is a junior subjective synonym of *Papilio irenea* Stoll, 1780), *Uraneis* Bates, 1868 (type species *Tharops hyalina* Butler, 1867) and *Esthemopheles* Röber, 1903 (type species *Esthemopheles lamprolenis* Röber, 1903, currently treated as a junior subjective synonym of *Uraneis ucubis* Hewitson, 1870) are not monophyletic with it, instead forming a clade (Fig. 23 red) sister to several genera (Fig. 23). To restore the monophyly, we propose that *Uraneis* Bates, 1868 **stat. rest.** is a valid genus and not a synonym of *Thisbe* Hübner, [1819]. The type species of *Uraneis* and *Esthemopheles* are closely related to each other (Fig. 23 red); e.g., their COI barcodes differ by 5.6% (37 bp), and, therefore, we keep *Esthemopheles* Röber, 1903 as a junior subjective synonym, but place it in synonymy with *Uraneis* Bates, 1868 and not with *Thisbe* Hübner, [1819].

Lenca Grishin, new subgenus

http://zoobank.org/3D0DB3C3-382E-4559-8C77-1698E6A854D3

Type species. *Lemonias lencates* Hewitson, 1875.

Definition. Genomic phylogeny reveals that a clade of *Pachythone* H. Bates, 1868 (type species *Pachythone erebia* Bates, 1868) species formerly placed in *Roeberella* Strand, 1932 (type species *Lemonias calvus* Staudinger, 1887) (Fig. 23 labeled aquamarine) is genetically differentiated from the rest at least at the subgenus level, e.g., COI barcodes of *Pachythone erebia* and *Pachythone lencates* (Hewitson, 1875) differ by 10% (66 bp). Therefore, this clade represents a new subgenus. This new subgenus differs from its relatives by the following combination of characters: forewings with a straight to slightly concave in the middle costal margin and a nearly hooked apex; wings are brown with darker-brown spots and dashes, beneath paler and with whiter areas and stronger brown spotting with at least some dark spots framed with white; and a dorsal hindwing with white stripes and spots and at least with a predominantly white anal fold. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cne9146.3.1:A1335C, cne9146.3.1:C1366T, cne81.7.1:G66A, cne81.7.1:T70A, cne10454.2.3:A303T; and in COI barcode: A88T, T220C, T281C, T349A, T475C.

Etymology. The name is formed from the type species and is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Lemonias lencates* Hewitson, 1875), *Roeberella flocculus* Brévignon & Gallard, 1993, *Roeberella floccus* Brévignon, 2013, *Roeberella heberti* P. Jauffret & J. Jauffret, 2007, and *Roeberella marajoara* P. Jauffret & J. Jauffret, 2007.

Parent taxon. Genus *Pachythone* H. Bates, 1868.

Pseudonymphidia Callaghan, 1985 is a subgenus of *Pachythone* H. Bates, 1868

Currently treated as a genus, *Pseudonymphidia* Callaghan, 1985 (type species *Emesis clearista* Butler, 1871) includes species that are phenotypically similar to species in the subgenus *Lenca* **subgen. n.** (type species *Lemonias lencates* Hewitson, 1875) of *Pachythone* H. Bates, 1868 (type species *Pachythone erebia* Bates, 1868), and all these species are differentiated genetically from each other at the subgenus level (Fig. 23 blue), e.g., COI barcodes of the type species of *Pseudonymphidia* and *Pachythone* differ by 9% (59 bp). Therefore, we propose that *Pseudonymphidia* Callaghan, 1985 **stat. nov.** is a subgenus of *Pachythone* H. Bates, 1868.

Family Lycaenidae [Leach], [1815]

Virachola F. Moore, 1881 is a valid genus distinct from *Deudorix* Hewitson, 1863

Genomic phylogeny reveals that *Deudorix* Hewitson, 1863 (type species *Dipsas epijarbas* F. Moore, 1858) is not monophyletic and species placed in this genus belong to four different clades (Fig. 24 blue, red, green, and magenta). The first is the clade with the type species of *Deudorix*, thus corresponding to this genus (Fig. 24 blue). This clade is sister to several genera that include *Artipe* Boisduval, 1870 (*Papilio amyntor* Herbst, 1804, a junior homonym, the valid name of this species is *Papilio eryx* Linnaeus, 1771) and *Capys* Hewitson, 1865 (type species *Papilio alpheus* Cramer, 1777). The second clade, which is not monophyletic with *Deudorix*, corresponds to the genus *Virachola* F. Moore, 1881 (type species *Deudorix perse* Hewitson, 1863) (Fig. 24 green), which at times is considered a valid genus (Rawlins et al. 2020). Thus, our phylogeny offers decisive evidence for treating *Virachola* F. Moore, 1881, **stat. rest.** as a genus distinct from *Deudorix*. However, *Virachola* is closely related to *Artipe* and could potentially be treated as its subgenus—a possibility we leave for future investigation. Furthermore, only Asian species are included in *Virachola*. African species form a clade that is sister to *Capys*, and we assign them to this genus within a newly described subgenus, detailed below. This new subgenus of *Capys* corresponds to the third clade of species currently in *Deudorix* (Fig. 24 magenta). The fourth clade is sister to all members of this group of several genera (Fig. 24 red) and it corresponds to a new genus that is described next.

Ajenorix Grishin, new genus

http://zoobank.org/5E009C8E-3D24-44C7-BE28-D1772045AC3E

Type species. *Rapala hypargyria* Elwes, 1893.

Definition. Genomic phylogeny reveals that several species placed in *Deudorix* Hewitson, 1863 (type species *Dipsas epijarbas* F. Moore, 1858) are not monophyletic with it and instead form a clade sister to several other genera, such as *Bindahara* F. Moore, 1881 (type species *Hesperia phocides* Fabricius, 1793)

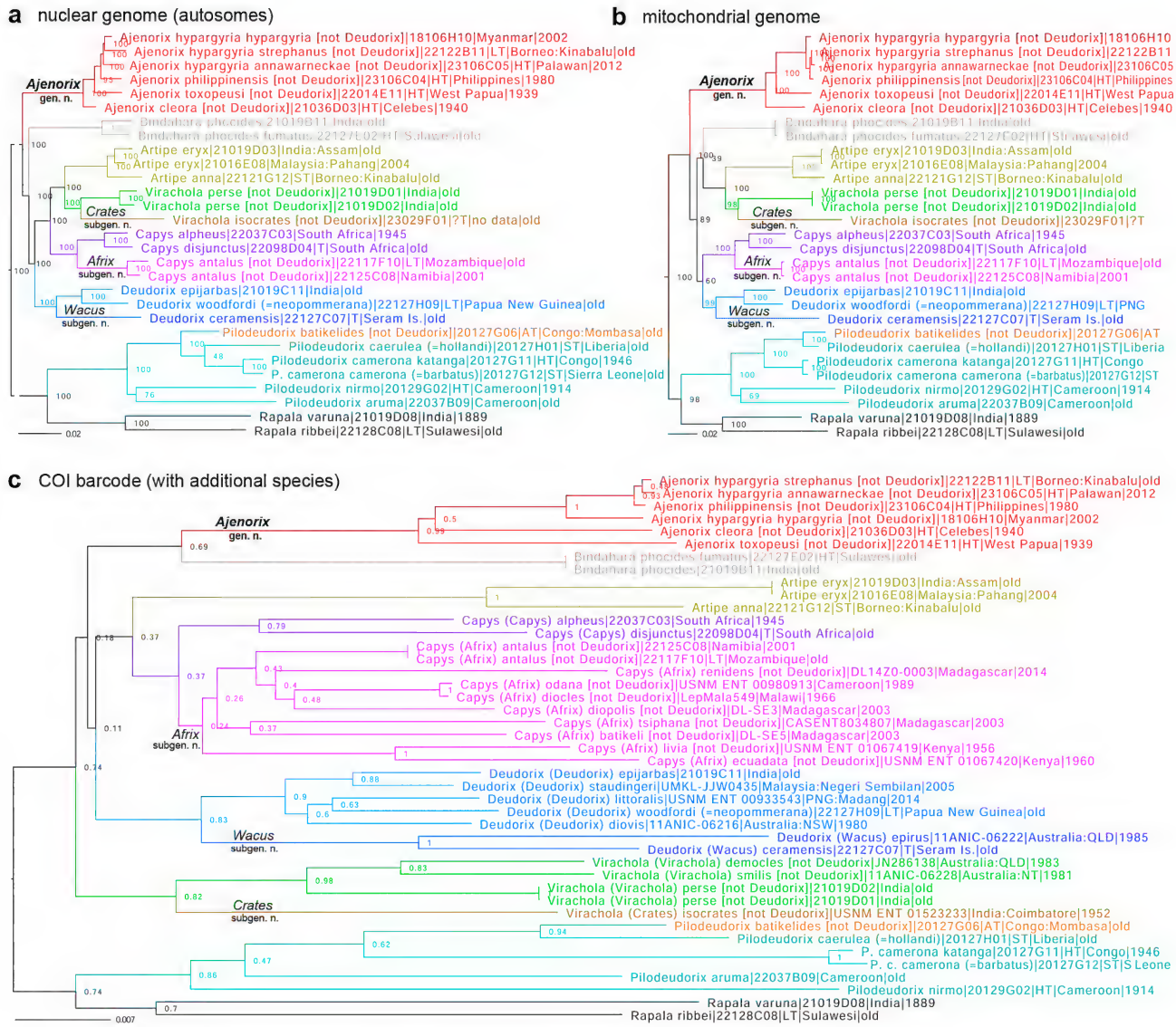

a nuclear genome (autosomes)
b mitochondrial genome
c COI barcode (with additional species)
Ajenorix gen. n.
Crates subgen. n.
Afrix subgen. n.
Wacus subgen. n.
Ajenorix hypargyria hypargyria [not Deudorix]|18106H10|Myanmar|2002
Ajenorix hypargyria strephanus [not Deudorix]|22122B11|LT|Borneo:Kinabalu|old
Ajenorix hypargyria annawarneckae [not Deudorix]|23106C05|HT|Palawan|2012
Ajenorix philippinensis [not Deudorix]|23106C04|HT|Philippines|1980
Ajenorix toxopeusi [not Deudorix]|22014E11|HT|West Papua|1939
Ajenorix cleora [not Deudorix]|21036D03|HT|Celebes|1940
Bindahara phocides 21019B11 India old
Bindahara phocides fumatus 22127E02 HT Sulawesi old
Artipe eryx|21019D03|India:Assam|old
Artipe eryx|21016E08|Malaysia:Pahang|2004
Artipe anna|22121G12|ST|Borneo:Kinabalu|old
Virachola perse [not Deudorix]|21019D01|India|old
Virachola perse [not Deudorix]|21019D02|India|old
Virachola isocrates [not Deudorix]|23029F01|?T|no data|old
Capys alpheus|22037C03|South Africa|1945
Capys disjunctus|22098D04|T|South Africa|old
Capys antalus [not Deudorix]|22117F10|LT|Mozambique|old
Capys antalus [not Deudorix]|22125C08|Namibia|2001
Deudorix epijarbas|21019C11|India|old
Deudorix woodfordi (=neopommerana)|22127H09|LT|Papua New Guinea|old
Deudorix ceramensis|22127C07|T|Seram Is.|old
Pilodeudorix batikelides [not Deudorix]|20127G06|AT|Congo:Mombasa|old
Pilodeudorix caerulea (=hollandi)|20127H01|ST|Liberia|old
Pilodeudorix camerona katanga|20127G11|HT|Congo|1946
P. camerona camerona (=barbatus)|20127G12|ST|Sierra Leone|old
Pilodeudorix nirmo|20129G02|HT|Cameroon|1914
Pilodeudorix aruma|22037B09|Cameroon|old
Rapala varuna|21019D08|India|1889
Rapala ribbei|22128C08|LT|Sulawesi|old
Deudorix (Deudorix) epijarbas|21019C11|India|old
Deudorix (Deudorix) staudingeri|UMKL-JJW0435|Malaysia:Negeri Sembilan|2005
Deudorix (Deudorix) littoralis|USNM ENT 00933543|PNG:Madang|2014
Deudorix (Deudorix) woodfordi (=neopommerana)|22127H09|LT|Papua New Guinea|old
Deudorix (Deudorix) diovis|11ANIC-06216|Australia:NSW|1980
Deudorix (Wacus) epirus|11ANIC-06222|Australia:QLD|1985
Deudorix (Wacus) ceramensis|22127C07|T|Seram Is.|old
Virachola (Virachola) democles [not Deudorix|JN286138|Australia:QLD|1983
Virachola (Virachola) smilis [not Deudorix]|11ANIC-06228|Australia:NT|1981
Virachola (Virachola) perse [not Deudorix]|21019D02|India|old
Virachola (Virachola) perse [not Deudorix]|21019D01|India|old
Virachola (Crates) isocrates [not Deudorix]|USNM ENT 01523233|India:Coimbatore|1952
Pilodeudorix batikelides [not Deudorix]|20127G06|AT|Congo:Mombasa|old
Pilodeudorix caerulea (=hollandi)|20127H01|ST|Liberia|old
P. camerona katanga|20127G11|HT|Congo|1946
P. c. camerona (=barbatus)|20127G12|ST|S Leone
Capys (Capys) alpheus|22037C03|South Africa|1945
Capys (Capys) disjunctus|22098D04|T|South Africa|old
Capys (Afrix) antalus [not Deudorix]|22125C08|Namibia|2001
Capys (Afrix) antalus [not Deudorix]|22117F10|LT|Mozambique|old
Capys (Afrix) renidens [not Deudorix]|DL14Z0-0003|Madagascar|2014
Capys (Afrix) odana [not Deudorix]|USNM ENT 00980913|Cameroon|1989
Capys (Afrix) diocles [not Deudorix]|LepMala549|Malawi|1966
Capys (Afrix) diopolis [not Deudorix]|DL-SE3|Madagascar|2003
Capys (Afrix) tsiphana [not Deudorix]|CASENT8034807|Madagascar|2003
Capys (Afrix) batikeli [not Deudorix]|DL-SE5|Madagascar|2003
Capys (Afrix) livia [not Deudorix]|USNM ENT 01067419|Kenya|1956
Capys (Afrix) ecuadata [not Deudorix]|USNM ENT 01067420|Kenya|1960

Fig. 24. Phylogenetic trees of selected Lycaenidae species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 447,723 positions, and **b)** the mitochondrial genome; and **c)** a BioNJ (Gascuel 1997) dendrogram constructed from COI barcodes using the phylogeny.fr server (Dereeper et al. 2008). Different genera are colored differently: *Ajenorix* **gen. n.** (red), *Bindahara* (gray), *Artipe* (olive), *Virachola* **stat. rest.** (green with subgenus *Crates* **subgen. n.** in brown), *Capys* (purple with subgenus *Afrix* **subgen. n.** in magenta), *Deudorix* (blue with subgenus *Wacus* **subgen. n.** in dark blue), and *Pilodeudorix* (cyan with *Pilodeudorix batikelides* **comb. nov.** labeled in orange). Ultrafast bootstrap (Minh et al. 2013) values are shown in (a) and (b), and regular bootstrap values (as fractions) from 100 replicates are shown in (c). In the COI barcode dendrogram (c), species are added from the BOLD database (Ratnasingham and Hebert 2007) (identification not checked) and their BOLD Sample ID (not equal to 8 symbols) or GenBank accession (8 symbols starting from a letter) are given. Sequences obtained by us are denoted by the sample ID of 8 symbols starting from a number. Gaps in branches indicate where a vertical slice of the tree was removed to reduce its horizontal dimension (to allow an increase in the font size), i.e., branches with gaps are longer than shown.

and *Capys* Hewitson, 1865 (type species *Papilio alpheus* Cramer, 1777), among others (Fig. 24 red), and, therefore, this clade corresponds to a new genus. This new genus differs from its relatives by having unusual for the group ventral wing patterns, i.e., instead of the typical grayish brown ground color with slightly darker bands framed with white lines separated into spots, species of the new genus are pearly gray with round brown spots, or creamy white with brown margins but without discal or postdiscal brown bands. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cce2070. 17.4:C477T, cce303125.12.1:A1164T, cce303125.12.1:T1191A, cce8301.4.10:A198G, cce8301.4.10:A243G; and COI barcode: A22T, A46T, A298T, A316T, A370T.

Etymology. In Spanish, deudo means relative, and ajeno means outsider, stranger, alien, or not-fitting, reflecting that this new genus does not fit within *Deudorix*: Ajeno + [~~Deudo~~]*rix*. According to the genomic phylogeny, this genus is an "outsider"—that is, sister to the rest of the clade. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Rapala hypargyria* Elwes, 1893), *Deudorix apayao* H. Schroeder & Treadaway, 1983, *Deudorix cleora* L. Miller & J. Miller, 1986, *Deudorix novellus* Yagishita, 2006, *Deudorix philippinensis* H. Schröder, Treadaway & Hayashi, 1981, and *Deudorix toxopeusi* Tennent, C. Müller & Rawlins, 2010.

Parent taxon. Tribe Deudorigini Doherty, 1886.

Afrix Grishin, new subgenus

http://zoobank.org/0EC2FE69-362B-4D26-BCAB-33E037003D40

Type species. *Dipsas antalus* Hopffer, 1855.

Definition. Genomic phylogeny reveals that African species currently placed in *Deudorix* Hewitson, 1863 (type species *Dipsas epijarbas* F. Moore, 1858) or *Virachola* F. Moore, 1881 (type species *Deudorix perse* Hewitson, 1863) are not monophyletic with these genera and instead form a clade sister to another African genus *Capys* Hewitson, 1865 (type species *Papilio alpheus* Cramer, 1777), being closely related to it (Fig. 24 purple and magenta); e.g., their COI barcodes differ by 4% (26 bp). Accordingly, we assign these species to the genus *Capys*, but, in light of some genetic divergence and pronounced differences in wing shape and pattern, we recognize them as a distinct subgenus. This new subgenus corresponds to "*Virachola*" of Stempffer (1967) who summarized its morphological characters. In brief, the aedeagus is typically longer; falces are shorter and thicker, in many species with a small apophysis; valvae are blade-shaped, frequently shorter, and are fused from the base, in some species for nearly their entire length, and are either long and terminally pointed or appear irregularly truncated (Larsen 2005); the hindwing with a prominent tornal lobe and a hair-like tail; the ventral forewing with a hair tuft and the dorsal hindwing with a small androconial spot at the base; the ventral wing pattern is frequently with rounder spots framed or filled by reddish (instead of grayish) scales; the dorsal hindwing is nearly all orange in males of many species. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cce3319. 2.2:T72A, cce3268.2.3:G82A, cce2518.2.9:T2032C, cce2518.2.9:A2061G, cce18900.2.2:T168C; and COI barcode: T38T, T304C, 400A, 514T, T547A.

Etymology. The name is a fusion of *Af*[rican] + [Deudo]*rix*, referring to the African distribution of this taxon. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Dipsas antalus* Hopffer, 1855), *Lycaena batikeli* Boisduval, 1833, *Deudorix caliginosa* Lathy, 1903, *Deudorix dariaves* Hewitson, 1877, *Deudorix dinochares* Grose-Smith, 1887, *Deudorix dinomenes* Grose-Smith, 1887, *Deudorix diocles* Hewitson, [1869], *Deudorix diopolis* Hewitson, [1878], *Deudorix* (*Virachola*) *ecaudata* Gifford, 1963, *Virachola*? *edwardsi* Gabriel, 1939, *Thecla galathea* Swainson, [1821], *Deudorix* (*Virachola*) *kayonza* Stempffer, 1956, *Lycaena livia* Klug, [1834], *Myrina lorisona* Hewitson, [1863], *Deudorix nicephora* Hulstaert, 1924, *Deudorix odana* Druce, 1887, *Hypolycaena renidens* Mabille, 1884, *Deudorix* (*Virachola*) *suk* Stempffer, 1948, *Virachola*

ufipa Kielland, 1978, *Deudorix ungemachi* Libert, 2004, *Deudorix* (*Virachola*) *vansomereni* Stempffer, 1951, and *Deudorix vansoni* Pennington, 1948.

Parent taxon. Genus *Capys* Hewitson, 1865.

Wacus Grishin, new subgenus

http://zoobank.org/2500C4A7-39A3-4A9A-A24A-46058014FE94

Type species. *Myrina epirus* C. Felder, 1860.

Definition. DNA sequence analysis reveals that several species of *Deudorix* Hewitson, 1863 (type species *Dipsas epijarbas* F. Moore, 1858) form a subclade genetically differentiated from others at the subgenus level (Fig. 24 blue and dark blue); e.g., their COI barcodes differ by 5.8% (38 bp), and, therefore, they represent a new subgenus. This new subgenus is differentiated from its relatives by its creamy-white ventral wings with dark brown discal and submarginal bands and margins, a longitudinal stripe in the anal area of the hindwing, and an orange stripe with dark spots (some blue-pupilled) extending from the tornus along the submarginal band, sometimes penetrating it. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cce3391.1.3:A1839G, cce49.4.1:A150T, cce8439.15.1:T595C, cce8439.15.1:T945A, cce2318.3.4:G270A, cce1567.13.2:T48T (not A), cce303136.3.19:T96T (not C); and COI barcode: T133A, A268G, T391A, T436A, T536C, A538T.

Etymology. The name is formed from [Ara]*wacus* Kaye, 1904, a Neotropical genus of Lycaenidae with a striped pattern in many species reminiscent of this new subgenus, but with additional stripes (thus a longer name). Furthermore, the name hints at a ventral wing pattern that is odd and eccentric (i.e., "wacky") for *Deudorix*. The name is a masculine noun in the nominative singular.

Species included. The type species (i.e., *Myrina epirus* C. Felder, 1860), *Deudorix ceramensis* Ribbe, 1901, *Deudorix eos* Hewitson, 1863, *Deudorix maudei* Joicey & Talbot, 1916, *Deudorix niepelti* Joicey & Talbot, 1922.

Parent taxon. Genus *Deudorix* Hewitson, 1863.

Crates Grishin, new subgenus

http://zoobank.org/9EE62E32-9133-4B8B-A664-FA552E1350FF

Type species. *Hesperia isocrates* Fabricius, 1793.

Definition. DNA sequence analysis reveals that *Virachola isocrates* (Fabricius, 1793) (type locality in India) forms a subclade genetically differentiated from its congeners at the subgenus level (Fig. 24 green and brown), e.g., COI barcodes differ by 5.5% (36 bp) between *V. isocrates* and *Virachola perse* (Hewitson, 1863) (type locality in North India), and, therefore, it represents a new subgenus. This new subgenus is differentiated from its relatives by straighter and less jagged margins of the discal bands on the ventral side of the wings (not as rounded, arc-like in every cell or even separated into spots as in typical *Virachola*), straighter and paler, more continuous darker bands being more similar to *Deudorix* Hewitson, 1863 (type species *Dipsas epijarbas* F. Moore, 1858), a more prominent orange lunule near the ventral hindwing tornus, and the lack of blue areas on the dorsal side of the wings. In DNA, a combination of the following characters is diagnostic in the nuclear genome: cce9657.10.14:T7356C, cce30130.8.1:C231T, cce30130.8.1:C243T, cce5405.12.5:A258G, cce4063.1.1:C81T, cce678.10.1:A132A (not G), cce2577.1.1:G282G (not A), cce2577.1.1:T291T (not C), cce4059.1.4:C252C (not T), cce3672.3.1:C126C (not T); and COI barcode: A22A, A114A, C274C, T505C, A562T, T604C.

Etymology. The name is formed from the type species name [iso]*Crates* and is a masculine noun in the nominative singular.

Species included. Only the type species (i.e., *Hesperia isocrates* Fabricius, 1793).

Parent taxon. Genus *Virachola* F. Moore, 1881.

Deudorix batikelides W. Holland, 1920 belongs to the genus *Pilodeudorix* H. H. Druce, 1891

Genomic phylogeny places the allotype of *Deudorix batikelides* W. Holland, 1920 (type locality in Congo, NVG-20127G06) (Fig. 24 labeled in orange) in the same clade with *Pilodeudorix* H. H. Druce, 1891 (type species *Pilodeudorix barbatus* H. H. Druce, 1891, which is regarded as a junior subjective synonym of *Sithon camerona* Plötz, 1880) (Fig. 24 cyan) and away from *Deudorix* Hewitson, 1863 (type species *Dipsas epijarbas* F. Moore, 1858) (Fig. 24 blue). While we were unable to find the holotype of *D. batikelides*, we use the allotype to represent this species and transfer *D. batikelides* from *Deudorix* to *Pilodeudorix*, forming *Pilodeudorix batikelides* (W. Holland, 1920), **comb. nov**.

Family Hesperiidae Latreille, 1809
Subfamily Eudaminae Mabille, 1877
Tribe Entheini Grishin, 2019

Phanus ecutinus Grishin, new species

http://zoobank.org/03E1BABC-DBC8-4A41-8438-2F0AEB2EA823

(Figs. 25 part, 26–27)

Definition and diagnosis. A female from Ecuador identified as *Phanus ecitonorum* Austin, 1993 (type locality in Brazil: Rondônia) by G. T. Austin after the dissection of genitalia appears as sister in the nuclear genome tree to several closely related species including *P. ecitonorum* (Fig. 25a), differing from it by 4.3% (28 bp) in the COI barcode, and, therefore, represents a new species. This species keys to *P. ecitonorum* in the key for females in Austin (1993) but differs from it by a narrower brown crevice in the hyaline spot in the forewing discal cell; smaller than the third, two subapical spots near the costa; and a larger dark brown ground color area between the forewing discal and postdiscal spots (e.g., the basal edge of the spot in the M_3-CuA_1 cell is more excavate). Female genitalia are heavily sclerotized, with broader (in ventral view) lamella antevaginalis and papillae anales; a concave near its posterior end ventral margin of the side lobe of lamella antevaginalis; a deeply notched in the middle lamella postvaginalis with arc-shaped and more evenly curved posterior margin on both sides of the notch, which is U-shaped, rounded anteriad and wider posteriad; and a wider, longer, and stronger sclerotized antrum (Fig. 27). Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1042.6.1: G360A, aly1651.12.7:C153A, aly1651.12.7:A168G, aly725.22.2:T45C, aly725.22.2:T54C, aly366.11.3: C489C (not T), aly366.11.3:A499A (not G), aly6841.72.2:T42T (not C), aly1931.14.4:T48T (not C), aly1139.62.12:T492T (not A); and COI barcode: A31C, C43T, T226C, T394C, T514C, T589C.

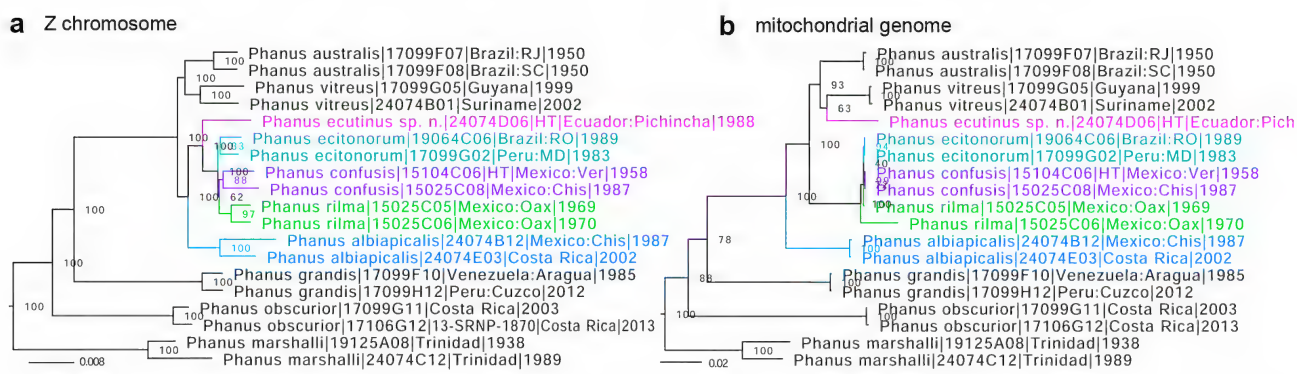


Fig. 25. Phylogenetic trees of *Phanus* species constructed from protein-coding regions in: **a)** the Z chromosome, based on 171,813 positions, and **b)** the mitochondrial genome: *P. ecutinus* **sp. n.** (magenta), *P. ecitonorum* (cyan), *P. confusis* Austin, 1993 (purple), *P. rilma* Evans, 1952 (green), and *P. albiapicalis* Austin, 1993 (blue). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

Fig. 26. *Phanus ecutinus* **sp. n.** holotype ♀ NVG-24074D06 in dorsal (left) and ventral (right) views, data in text.

Barcode sequence of the holotype. Sample NVG-24074D06, GenBank PV549987, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCCGGAATAGTAGGTACATCTTTAAGTTTATTAATTCGAACAGAATTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCATTTATTATAATTTTTTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTGGGTGCCCCAGACATAGCTTTCCCTCGAA
TAAATAATATAAGTTTTTGACTCCTCCCCCCATCATTAACTTTATTAATCTCAAGAAGAATTGTAGAAAATGGAGCCGGAACTGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
TCACCAAGGTTCATCTGTCGATTTAGCAATCTTTTCCTTACACTTAGCTGGAATTTCATCTATTTTAGGTGCAATTAATTTTATTACTACAATTATTAATATACGTATTAGAAATTTATCT
TTTGATCAAATACCCTTATTCATTTGAGCCGTTGGAATTACTGCTTTATTATTATTACTTTCTCTTCCTGTTTTAGCAGGAGCTATTACAATACTTTTAACTGACCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTCTTTACCAACATTTATTT

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 26 (genitalia Fig. 27), bears the following seven printed (text in italics handwritten) rectangular labels, six white: [ECUADOR | Pichincha Province | Hotel Tinalandia | 12 km E Santa | Domingo de los | Colorados | 750–850 m | 13 May 1988 | leg G&A Austin], [Phanus vitreus | (Stoll) | det GT Austin 199*1*], [Genitalia Vial | GTA-*2247*], [Phanus ecitonorum | Austin | det. G. T. Austin | 1992], [G T Austin colln | MGCL Acc. | 2004-5], [DNA sample ID: | NVG-24074D06 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Phanus ecutinus | Grishin].

Fig. 27. Genitalia of *P. ecutinus* **sp. n.** holotype ♀ NVG-24074D06 in ventral (left) and ventrolateral (right) views.

Type locality. Ecuador: Pichincha, Santo Domingo de los Colorados, Tinalandia Lodge.

Etymology. The name is given for the type locality and is a fusion of *Ecu*[ador] + *Tin*[alandia] + *us*. The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected west of the Andes in northern Ecuador.

Entheus zeus **Grishin, new species**

http://zoobank.org/D6F4DA98-5D23-4697-90C1-DF47DF63DC0A

(Figs. 28 part, 29–30, 50 part, 51a)

Definition and diagnosis. Genomic analysis of *Entheus* Hübner, [1819] (type species *Papilio peleus* Linnaeus, 1763, which is a junior subjective synonym of *Papilio priassus* Linnaeus, 1758) reveals that two males from the Amazonian region in Brazil are close to *Entheus gentius* (Cramer, 1777) (type locality in Suriname, neotype sequenced as RMNH.INS.907819) but are genetically differentiated from it at the species level (Fig. 28); e.g., their COI barcodes differ by 1.7% (11 bp). Therefore, these specimens represent a new species. This new species is similar to *E. gentius* (as defined by its neotype) and keys to it

(B.10.3) in Evans (1952), sharing (in males) a broad dark-brown (nearly black) hindwing border expanding its width towards the tornus, even broader on the ventral side, orange scales invading the dark border near the dorsal forewing tornus, thus the boundary between orange and dark is not sharply defined, and a tawny turning black towards the end hindtibial tuft; but differs from it by a narrower forewing orange discal band without noticeable hyalinity in the discal cell, even fuzzier boundary between orange and dark brown on the dorsal hindwing, and browner (less black) dark color; the valva is narrower than in *E. gentius* with a more extended harpe. Due to unexplored individual variation of this species and the lack of known females, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly6841.51.2:A1224G, aly6841.51.2:T1386A, aly6841.51.2:A1416G, aly8478.7.3:G57A, aly8478.7.3:C36G; and COI barcode: T278T, 376T, T463C, A517C, T535C.

Barcode sequence of the holotype. Sample NVG-22017H08, GenBank PV549988, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGACTATTAATTCGAACTGAATTAGGAACCCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGTTTTGGTAATTGATTAGTACCTTTAATATTAGGAGCTCCAGATATAGCTTTCCCCCGTA
TAAATAATATAAGTTTTTGACTTTTACCCCCATCATTAACATTATTAATTTCAAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCCCCACTATCAGCTAATATTGC
ACATCAAGGTTCTTCTGTAGATTTAGCAATTTTTTCCCTTCATTTAGCTGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAATTAGAAATTTATCA
TTTGATCAAATACCACTATTTGTATGAGCAGTCGGTATTACTGCATTACTCTTATTATTATCTTTACCAGTATTAGCTGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGTGGGGGAGATCCAATTCTTTATCAACATTTATTT

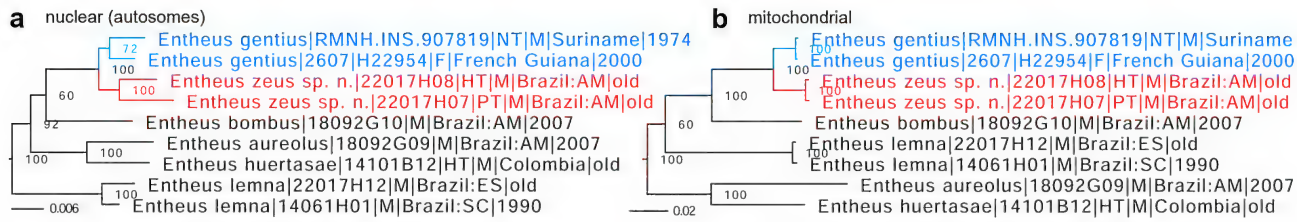


Fig. 28. Phylogenetic trees of *Entheus gentius* group species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome: *E. gentius* (blue) and *E. gentius* **sp. n.** (red).

Fig. 29. *Entheus zeus* **sp. n.** holotype ♂ NVG-22017H08 in dorsal (left) and ventral (right) views, data in text. The inset shows the hindtibial tuft enlarged two times compared to the specimen (scale not given).

Type material. Holotype: ♂ deposited in the Zoologische Staatssammlung München, Germany (ZSMC), illustrated in Figs. 29 and 51a, bears the following three printed rectangular labels, two white: [Amazonas | Coll Fassl | in Coll. Arp], [DNA sample ID: | NVG-22017H08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | zeus Grishin]. **Paratypes:** 2♂♂: 1♂ NVG-22017H07 with the same data as the

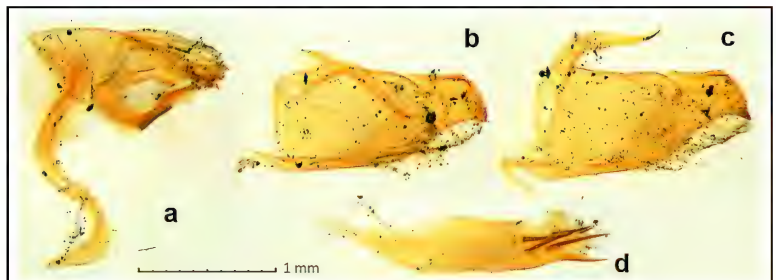


Fig. 30. Genitalia of *Entheus zeus* **sp. n.** paratype ♂, slide 488 (views): **a)** genitalia with valvae and aedeagus detached (left lateral); **b, c)** valvae (lateral); **d)** aedeagus (left lateral).

holotype and 1♂ NVG-15099B11 Brazil, Amazonas, Madeira River, Manicoré, Nov-1923, Bruno Poll leg., genitalia slide No. 488 (Fig. 30) [CMNH].

Type locality. Brazil: Amazonas, likely mid-Amazon.

Etymology. We arrived at the name starting from "fuzzy" for the blurred (compared to its relatives) border between dark-brown and orange by the dorsal hindwing tornus of this species: *fuzz*[y]+[Enth]*eus* → [fuz]*zeus* → *zeus*, and it seems suitable for this bright-orange species fitting to be the king. The name is treated as a masculine noun in apposition.

Distribution. Currently known only from the type locality in the Amazonian region.

Comment. We have not attempted to remount the old genitalia slide No. 488 (currently in the CMNH cabinet with genitalia slides, mostly prepared by R. Williams) and illustrate genitalia here in their original condition, as mounted, without cleaning (Fig. 30).

Entheus talaus (Linnaeus, 1763) is a species distinct from *Entheus priassus* (Linnaeus, 1758)

Genomic analysis reveals that sequenced specimens that we identified as *Entheus priassus* (Linnaeus, 1758) (type locality stated as "Indiis", likely in or around Suriname) partition into three species (Fig. 31, marked as yellow-highlighted 1, 2, and 3 above their clades). The first species is more widespread with specimens sequenced from Venezuela, Guyana, Suriname, and French Guiana. The second and the third species were sequenced from French Guiana (and one specimen from Brazil: Amapá) and Guyana, respectively (Fig. 32). We note that these distribution records are based only on several sequenced specimens and are necessarily incomplete, to be addressed by more comprehensive sequencing.

The first species is characterized by males with wider yellow-orange bands and more developed hyalinity along the distal margin of the discal band, and females with more restricted pale spotting, including the discal spot on the dorsal hindwing and wider separation between white forewing spots in the discal cell and the cell CuA_1-CuA_2, with the latter spot being out of alignment with (tilted distad from) the former. This phenotype matches best the lectotype illustration of *Papilio peleus* Linnaeus, 1763 (type

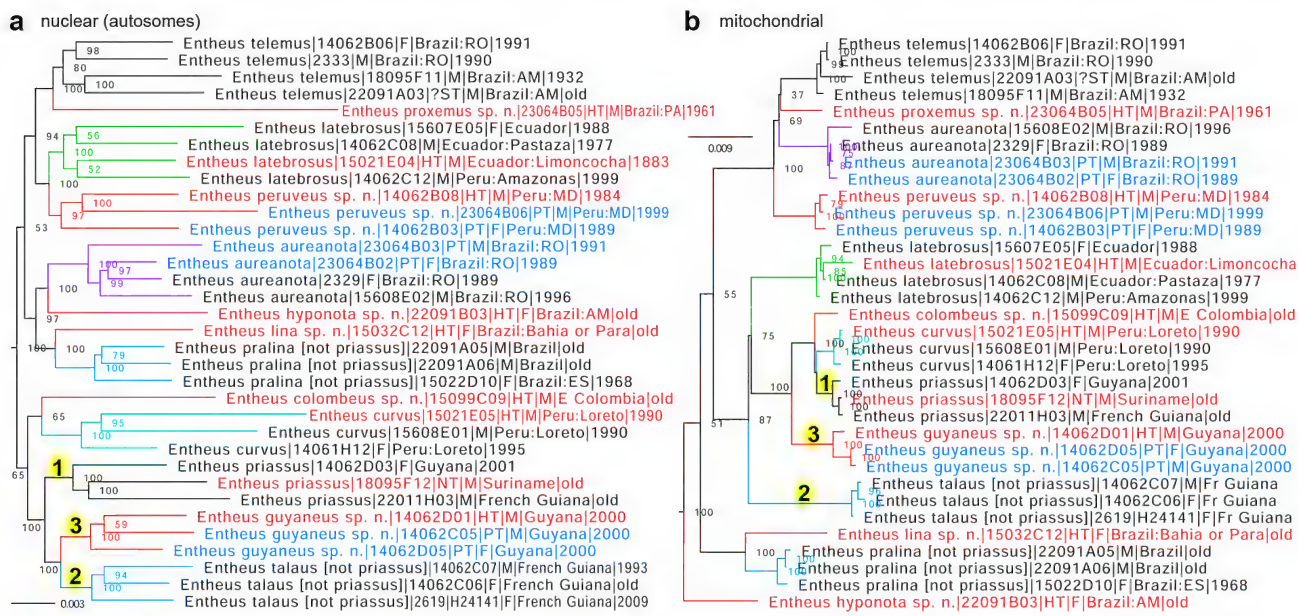


Fig. 31. Phylogenetic trees of *Entheus priassus* group species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,580,949 positions, and **b)** the mitochondrial genome. Primary and secondary type specimens are labeled in red and blue, respectively. Branches of new taxa are shown in red, and those with subspecies-to-species status change in blue. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Clades of more recently proposed species are colored: *E. latebrosus* (green), *E. aureanota* (purple), and *E. curvus* (cyan). The clades corresponding to the three species discussed in the text in detail are numbered 1, 2, and 3 with a yellow highlight.

locality stated as "Indiis", likely in the Guianas), a male, by Clerck ([1764]) and the illustration of *Entheus cramerianus* Mabille, 1898 (type locality in Suriname and French Guiana) syntype from Suriname in Stoll (1782), a female. We note that in our interpretation of the original description (Mabille 1898), the type series of *E. cramerianus* consists of females only: the specimen identified as *Papilio talaus* and illustrated in fig. C, pl. 393 in Stoll (1782), referred to as "*Pap. Talaus* Cram. pl. 293, nec Lin" (293 is a lapsus for 393) by Mabille (1898) and female specimens considered to belong to this species and inspected by Mabille (1898), which he referred to as "On le reçoit de la Guyane assez fréquemment" ("we receive it from [French] Guiana quite frequently"). For the stability of nomenclature, we maintain the synonymy between *P. peleus* and *Papilio priassus* Linnaeus, 1758 (type locality stated as "Indiis", likely in or around Suriname), described from male(s), not illustrated, the original description agrees with males of any of these three (and many other *Entheus*) species, and identify this first species as *P. priassus*. Neotypes for these taxa are designated below to preserve this synonymy in prevailing usage.

The second species is characterized by narrower and straighter at margins orange bands with less hyalinity in males, and females with larger white spots, including the discal spot on the dorsal hindwing and better aligned, larger spots in the forewing discal cell and the cell CuA_1-CuA_2, with these two spots and the spot in the cell CuA_2-1A+2A forming a white band. This phenotype agrees best with the lectotype illustration of *Papilio talaus* Linnaeus, 1763 (type locality stated as "Indiis", likely in or around Suriname), a female, by Clerck ([1764]), a syntype illustration of *Peleus aeacus* Swainson, 1831 (type locality in South America), a male, by Swainson (1831) and a syntype of *Phareas serenus* Plötz, 1883 (type locality not specified) from the Weymer collection that we located in MFNB. Therefore, we propose that *Entheus talaus* (Linnaeus, 1763), **stat. rest.** is a species distinct from *Entheus priassus* (Linnaeus, 1758); *Papilio peleus* Linnaeus, 1763 with *Entheus cramerianus* Mabille, 1898 are junior subjective synonyms of *Entheus priassus*; and *Peleus aeacus* Swainson, 1831 with *Phareas serenus* Plötz, 1883 are junior synonyms of *Entheus talaus*. This treatment appears most consistent with the available literature on these taxa, and lectotypes or neotypes for most of them are designated accordingly in the sections below.

The third species, from Guyana, differs by the doublet of semi-hyaline spots in forewing cells M_1-M_2 and M_2-M_3 being stronger offset distad from the triplet of the subapical spots (in a female, this doublet is narrower compared to other species) and the semi-hyaline spot in the cell M_3-CuA_1 only narrowly connected to the discal orange band (among other characters) and is new, described below. Genomic trees focusing on this subgroup of three species are shown in Fig. 32.

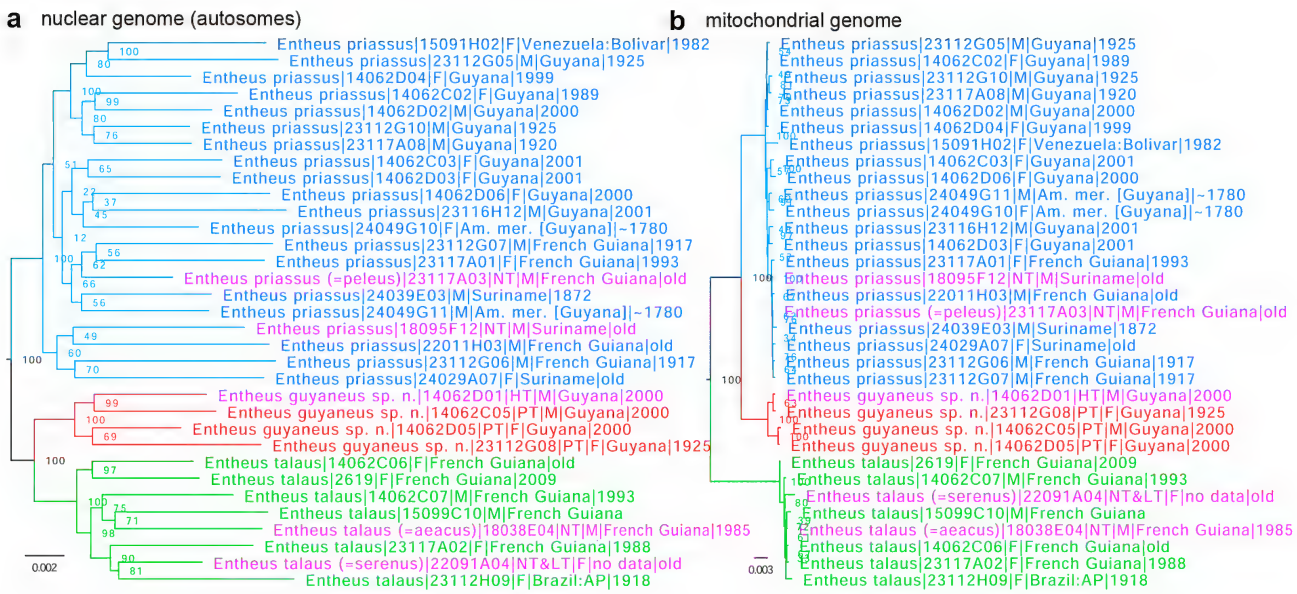


Fig. 32. Phylogenetic trees of *Entheus priassus* (blue), *Entheus guyaneus* **sp. n.** (red), and *Entheus talaus* (green) constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 2,495,064 positions, and **b)** the mitochondrial genome. Primary type specimens are labeled in magenta. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

a
b
1 cm
c
d
341
Weymer
Talaus
Cr393
Talaus var
Coll. Weymer
60 : 2.
1 cm
DNA sample ID:
NVG–22091A04
c/o Nick V. Grishin

Fig. 33. (see previous page). Primary type specimens of *Entheus* designated in this work in dorsal (left) and ventral (right) views, data in text, insets show hindtibial tuft enlarged two times compared to specimens (scale not given): **a)** neotype of *Papilio priassus* ♂ NVG-18095F12; **b)** neotype of *Papilio peleus* ♂ NVG-23117A03; **c)** neotype of *Peleus aeacus* ♂ NVG-18038E04; **d)** lectotype of *Phareas serenus* ♀ NVG-22091A04 that is also the neotype of *Papilio talaus*, with its labels shown below and reduced by a quarter in size compared to specimens. The scale for labels is shown below them, and the scale for specimens is in the middle of the figure.

Lectotype designation for *Phareas serenus* Plötz, 1883

Phareas serenus Plötz, 1883 (Weymer in litt.) was described from an unstated number of specimens from unknown localities. The description given as part of the identification key (Plötz 1883) can be translated from German as "The hindwing is broadened from the anal angle to vein 4, above with an oval oblique white discal spot, beneath broadly black almost along the entire costal margin. The forewing above at the inner margin of the discal cell with a red longitudinal streak extending to the base, and the row of spots in cells 4–9 is interrupted at vein 6, beneath the base is dark gray." Only females agree with this description. We located and sequenced (NVG-22091A04) a single syntype of *P. serenus* in the MFNB collection (Figs. 33d and 51d). The syntype is from the Weymer collection, is labeled as "… Serenus Wmr i. l" (for "in litteris"), and was seen by Plötz according to its label, thus agreeing with all the details of the original description. This is likely the only specimen on which the description of *P. serenus* was based. However, avoiding the assumption of the holotype, to define the taxonomic identity of the name *P. serenus* objectively, N.V.G. hereby designates a syntype in the MFNB collection, a female illustrated in Figs. 33d and 51d (genitalia Fig. 34a–c) and bearing the following eight rectangular white labels (4th and the last three printed, others handwritten): [341 | Weymer], [Talaus | Cr393c], [Talaus var | Serenus Wmr i. l | 341 best. v. Plötz.], [Coll. Weymer], [60:2.], [DNA sample ID: | NVG-22091A04 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23082A08 | c/o Nick V. Grishin], [genitalia: | NVG240817-38 | c/o Nick V. Grishin] as the **lectotype** of *Phareas serenus* Plötz, 1883. According to the 3rd label, the name for this species proposed by Weymer in correspondence ("i. l") is *serenus*, and this specimen was "identified" (probably just inspected in this case) by Plötz ("best[immt]. v[on]. Plötz"). The number 341 is likely an unpublished Weymer's collection specimen number, or maybe a specimen No. 341 inspected by Plötz in Weymer's collection. The 5th label "60:2." gives the number for *Entheus cramerianus* Mabille, 1898 (type locality in South America) in Mabille's catalog (1903), meaning that this specimen was identified as *E. cramerianus* by a curator of the MFNB collection. The first DNA sample refers to the extraction from a leg and the second is from the abdomen prior to genitalia dissection. The lectotype is missing the left antenna, and every wing but the right hindwing is chipped once at its outer margin. On the basis of genomic comparison, we deduce that the type locality of *P. serenus* is in the Amazonian region, possibly in Brazil: Pará. The COI barcode sequence of the lectotype, sample NVG-22091A04, GenBank PV549989, 658 base pairs, is:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTGGGAGCCCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTCTACCCCCCTCTATCTGCCAATATTGC
CCATCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCCGTATTAGCAGGCGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCCGCAGGAGGAGGGGATCCTATTCTTTATCAACACTTATTT

Neotype designation for *Papilio priassus* Linnaeus, 1758

The name *Papilio priassus* Linnaeus, 1758 was proposed from an unstated number of specimens from "Indiis" and the original description can be translated from Latin as "wings rounded, uniformly black; the forewings with two tawny bands joined by a third smaller spot" (Linnaeus 1758). Several years after the description, this species was re-described from specimen(s) in the collection of Queen Ludovica Ulrika (Linnaeus 1764). Although this description is longer, it is unclear whether it applies to this species and whether the type series was among Ulrika's specimens. Currently, and since Aurivillius (1882), two other taxa, *Papilio talaus* Linnaeus, 1763 (type locality in "Indiis", described from a female) and *Papilio peleus* Linnaeus, 1763 (type locality in "Indiis", described from a male) have been treated as junior subjective synonyms of *P. priassus* (Evans 1952; Mielke 2005).

Fig. 34. Female genitalia of *Entheus* primary types, data in text (ductus bursae and bursa copulatrix not shown): **a–c)** *E. talaus* neotype and, simultaneously, *Phareas serenus* lectotype NVG-22091A04; **d–f)** *E. hyponota* **sp. n.** holotype NVG-22091B03; **g–i)** *E. lina* **sp. n.** holotype NVG-15032C12; **j–k)** *E. ecuadius* **sp. n.** holotype NVG-14062C11 in different views: **a**, **d**, **g**, **j**) ventral; **b**, **e**, **h**) left ventrolateral; **c**, **f**, **i**, **k**) right ventrolateral.

To learn more about the taxonomic identity of this species, we searched for its syntypes among Hesperiidae holdings in all major collections that are listed in the Acknowledgments section. In particular, N.V.G. paid special attention to possible syntypes in the NHRS collection, where Clerck's specimens are preserved, because lectotypes of *P. peleus* and *P. talaus* are specimens illustrated by Clerck ([1764]). We failed to find syntypes, which agrees with the statement in Honey and Scoble (2001) that they were lost. Not finding syntypes, we proceeded with the neotype designation. There is an exceptional need for the neotype of *P. priassus* to define this taxon objectively because several cryptic species are present among its relatives and its type locality is poorly defined ("Indiis"). Because type specimens of many Lepidoptera names proposed in the 18th century were from Suriname, it seems plausible that at least part of the type series of *P. priassus* was from Suriname (Honey and Scoble 2001). Therefore, we selected a Surinamese specimen, a male, which agrees with the original description and the current application of the name, as the neotype. Hereby, N.V.G. designates the specimen in MTD shown in Figs. 33a and 51b (DNA sample NVG-18095F12) as the **neotype** of *Papilio priassus* Linnaeus, 1758.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *P. priassus*, which is necessary because undescribed

species are present among its close relatives, and to define the type locality that was stated in the original description as "Indiis"; **75.3.2.** The characters to differentiate this taxon from others are given in the original description (see the translation above), and we interpret them as: rounded and uniformly dark-brown wings, discal and subapical orange bands on the forewings, and an orange spot in between them connected to the discal band; **75.3.3.** The neotype specimen is a male bearing four rectangular white labels (1st handwritten, others printed): [Surin.], [Staatl. Museum für | Tierkunde Dresden], [Stauding.& Bang-Haas | Dresden, Ankauf 1961], [DNA sample ID: | NVG-18095F12 | c/o Nick V. Grishin] and shown in Figs. 33a and 51b; the neotype has a tear at the costal margin near the apex on each forewing and is missing the left antenna and the terminal third of the right antenna; **75.3.4.** We failed to find syntypes of *P. priassus* among Hesperiidae holdings in all collections we visited (see Acknowledgments for their list) and therefore, taking into account similarly negative reports in literature (Honey and Scoble 2001), believe that they were lost; **75.3.5.** The neotype closely agrees with the original description and all other information published about *P. priassus*, as evidenced by observing the characters stated in the original description translated above in the neotype photographs in Figs. 33a and 51b; **75.3.6.** The neotype is from Suriname and the original type locality given as "Indiis" is deemed to include this area, frequently referring—for non-insular New World specimens—to the Guianas in general and Suriname in particular, (Honey and Scoble 2001); **75.3.7.** The neotype is in the Museum für Tierkunde, Dresden, Germany (MTD). As a result of the neotype designation, the type locality of *P. priassus* becomes Suriname. The COI barcode sequence of the neotype, sample NVG-18095F12, GenBank PV549990, 658 base pairs, is:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTGGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCCGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTCTTTATCAACACTTATTT

Neotype designation for *Papilio talaus* Linnaeus, 1763

The lectotype of *Papilio talaus* Linnaeus, 1763 (type locality in "Indiis") has been designated by Aurivillius (1882) as the specimen illustrated on the pl. 45, fig. 1 by Clerck ([1764]), The illustration of the lectotype shows a female with larger white spots than in its relatives, including the discal spot on the dorsal hindwing and better aligned larger spots in the forewing discal cell and the cell CuA_1-CuA_2, with these two spots and the spot in the cell CuA_2-1A+2A forming a white band. To learn more about the taxonomic identity of this species, we searched for its lectotype among Hesperiidae holdings in all major collections that are listed in the Acknowledgments section. In particular, N.V.G. paid special attention to *Entheus* Hübner, [1819] specimens in the NHRS collection, where Clerck's specimens are preserved, because the lectotype is a specimen illustrated by Clerck ([1764]). The lectotype was not found, which agrees with the statement in Honey and Scoble (2001) that they have not located Linnaean specimens of this species. Not finding the lectotype, we proceeded with the neotype designation. There is an exceptional need for the neotype of *P. talaus* to define this taxon objectively because several cryptic species are present among its relatives and its type locality is poorly defined ("Indiis"). For the neotype, we selected a female, which looks particularly similar in wing patterns to Clerck's illustration among the specimens we examined. This specimen is the lectotype of *Phareas serenus* Plötz, 1883 (type locality in South America: the Amazonian region). Hereby, N.V.G. designates the lectotype of *P. serenus* in MFNB shown in Figs. 33d and 51d (DNA sample NVG-22091A04) as the **neotype** of *Papilio talaus* Linnaeus, 1763. As a result of the neotype designation, *Phareas serenus* Plötz, 1883 becomes a junior objective synonym of *Papilio talaus* Linnaeus, 1763.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *P. talaus*, which is necessary because new species are present among its close relatives, and to define the type locality that was stated in the original description as "Indiis"; **75.3.2.** The characters to differentiate this taxon from others are revealed from the illustrations of its lectotype in Clerck ([1764]) and are given above, i.e., larger white spots, such as the discal spot on

the dorsal hindwing and better aligned spots in the forewing discal cell and the cell CuA_1-CuA_2: these two spots and the spot in the cell CuA_2-1A+2A form a white band, two white spots are present in the forewing cell CuA_2-1A+2A of the lectotype, white area on the ventral hindwing reaches the inner margin and is angled rather than rounded distad of the discal cell; **75.3.3.** The neotype specimen is a female bearing the following eight rectangular white labels (4^{th} and the last three printed, others handwritten): [341 | Weymer], [Talaus | Cr393c], [Talaus var | Serenus Wmr i. l | 341 best. v. Plötz.], [Coll. Weymer], [60:2.], [DNA sample ID: | NVG-22091A04 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23082A08 | c/o Nick V. Grishin], [genitalia: | NVG240817-38 | c/o Nick V. Grishin] and shown in Figs. 33d and 51d; this specimen is also the lectotype of *Phareas serenus* Plötz, 1883 (see the lectotype designation section above for additional details about this specimen and its labels); **75.3.4.** We failed to find the lectotype and paralectotypes of *P. talaus* among Hesperiidae holdings in all collections we visited (see Acknowledgments for their list) and therefore, taking into account similarly negative reports in literature (Honey and Scoble 2001), believe that they were lost; **75.3.5.** The neotype closely agrees with the illustration of the *P. talaus* lectotype in all characters, as evidenced by comparing the neotype shown in Figs. 33d and 51d with the illustration on the pl. 45, fig. 1 in Clerck ([1764]) and the characters for this taxon listed above (75.3.2.), e.g., even a semi-hyaline spot by the 1A+2A vein on the forewing is present in the neotype and lectotype; **75.3.6.** The neotype is from unknown locality identified as in the Amazonian region of South America (possibly in Brazil: Pará) by genomic analysis and the original type locality given as "Indiis" is deemed to include this area, because for non-insular specimens from the New World it typically referred to the Guianas region (Honey and Scoble 2001). The type locality will be further refined by genomic comparisons with additional specimens from across South America; **75.3.7.** The neotype is in the Museum für Naturkunde, Berlin, Germany (MFNB). The COI barcode sequence of the neotype is given above in the section "Lectotype designation for *Phareas serenus* Plötz, 1883."

Neotype designation for *Papilio peleus* Linnaeus, 1763

The lectotype of *Papilio peleus* Linnaeus, 1763 (type locality in "Indiis") has been designated by Aurivillius (1882) as the specimen illustrated on pl. 45, fig. 5 by Clerck ([1764]). The illustration of the lectotype shows a male with wider yellow-orange bands and more developed hyalinity along the distal margin of the discal band. To learn more about the taxonomic identity of this species, we searched for its lectotype among Hesperiidae holdings in all major collections that are listed in the Acknowledgments section. In particular, N.V.G. paid special attention to *Entheus* Hübner, [1819] specimens in the NHRS collection, where Clerck's specimens are preserved, because the lectotype is a specimen illustrated by Clerck ([1764]). The lectotype was not found, which agrees with the results by Honey and Scoble (2001) who have not found type specimens of this species. Not finding the lectotype, we proceeded with the neotype designation. There is an exceptional need for the neotype of *P. peleus* to define this taxon objectively because several cryptic species are present among its relatives and its type locality is poorly defined ("Indiis"). For the neotype, we selected a male, which looks most similar in wing patterns to Clerck's illustration among the specimens we examined. Clerck's illustration shows an unusual character: the semi-hyaline orange-yellow spot in the forewing cell M_3-CuA_1 reaches (and even overlaps with in some copies of the book) the subapical semi-hyaline band. Because this character seems to be present as an unusual aberration only, and is variably shown in different copies of the book by Clerck ([1764]), we hypothesize that it might have been an artifact of the drawing. Nevertheless, we selected a specimen with a comparatively smaller gap between the spot and the band. Hereby, N.V.G. designates the specimen in USNM shown in Figs. 33b and 51c (DNA sample NVG-23117A03) as the **neotype** of *Papilio peleus* Linnaeus, 1763.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *P. peleus*, which is necessary because new species are present among its close relatives, and to define the type locality that was stated in the original description as "Indiis"; **75.3.2.** The characters to differentiate this taxon from others are revealed from the illustrations of its lectotype in Clerck ([1764]) and are given above, i.e., broader forewing orange bands with more extensive hyalinity along the distal margin of the discal band; **75.3.3.** The neotype specimen is a male

bearing three rectangular printed white labels: [St. Jean, | Maroni, | F. Guiana], [Collection | WmSchaus], [DNA sample ID: | NVG-23117A03 | c/o Nick V. Grishin] and shown in Figs. 33b and 51c; the neotype's antennae overlap wings above, and the right hindwing has a thin linear scratch from the apex towards the inner margin on the ventral side; **75.3.4.** We failed to find the lectotype and paralectotypes of *P. peleus* among Hesperiidae holdings in all collections we visited (see Acknowledgments for their list) and therefore, taking into account similarly negative reports in literature (Honey and Scoble 2001), believe that they were lost; **75.3.5.** The neotype closely agrees with the illustration of the *P. peleus* lectotype in nearly all characters, as evidenced by comparing the neotype shown in Figs. 33b and 51c with the illustration on pl. 45, fig. 5 in Clerck ([1764]) and the characters for this taxon listed above (75.3.2.); **75.3.6.** The neotype is from French Guiana and the original type locality given as "Indiis" is deemed to cover this area because for non-insular specimens from the New World, it typically referred to the Guianas region (Honey and Scoble 2001); **75.3.7.** The neotype is in the National Museum of Natural History, Washington, DC, USA (USNM). As a result of the neotype designation, the type locality of *P. peleus* becomes French Guiana: Saint-Jean-du-Maroni. The COI barcode sequence of the neotype, sample NVG-23117A03, GenBank PV549991, 658 base pairs, is:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTGGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTGGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCCGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTCTTTATCAACACTTATTT

Lectotype designation for *Peleus aeacus* Swainson, 1831

The name *Peleus aeacus* Swainson, 1831 (type locality at least in Suriname) was proposed from an unstated number of specimens that, in addition to the specimen shown on pl. 284, fig. F in Cramer (1780), included the specimen illustrated in Swainson (1831). It is not a replacement name, but a name that, according to Swainson, included Cramer's concept of *Papilio peleus* Linnaeus, 1763. Cramer's specimen, although it was included in the type series, does not agree with the original description, because the forewing discal band is not "united to a spot" between the bands, and is not conspecific with the specimen illustrated by Swainson (1831). Therefore, Swainson's specimen better represents the author's concept of this species. To stabilize nomenclature and define the name *P. aeacus* objectively, N.V.G. hereby designates a syntype illustrated on pl. 75, fig. 2 in Swainson (1831) as the **lectotype** of *Peleus aeacus* Swainson, 1831. The provenance of this specimen remains unknown, but this phenotype has been known from South America (most probably the Guianas region), which becomes the type locality of this taxon. This lectotype designation is necessary to exclude Cramer's specimen as the name bearer.

Neotype designation for *Peleus aeacus* Swainson, 1831

The illustration of the lectotype of *Peleus aeacus* Swainson, 1831 (type locality in South America, likely in the Guianas) reveals that it is a species characterized by males with forewing orange bands that are narrower, straighter at the margins, and exhibit less hyalinity. To learn more about the taxonomic identity of this species, we searched for its lectotype among Hesperiidae holdings in all major collections that are listed in the Acknowledgments section. In particular, the remainder of Swainson's collection of insects is preserved at the University of Cambridge, UK (Anonymous 2025). We searched the collection catalogue and did not find any *Entheus* specimens. Not finding the lectotype, we proceeded with the neotype designation. There is an exceptional need for the neotype of *P. aeacus* to define this taxon objectively because several cryptic species are present among its relatives, and its type locality is not specified in the original description (Swainson 1831). For the neotype, we selected a male, which, among the specimens we examined, looks most similar in wing patterns to the illustration of the lectotype on pl. 75, fig. 2 by Swainson (1831). Hereby, N.V.G. designates the specimen in SMF shown in Fig. 33c (DNA sample NVG-18038E04) as the **neotype** of *Peleus aeacus* Swainson, 1831.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *P. aeacus*, which is necessary because new species are

present among its close relatives, and to define the type locality that was not stated in the original description; **75.3.2.** The characters to differentiate this taxon from others are revealed from the original description and the illustration of its lectotype on pl. 75, fig. 2 in Swainson (1831) and are given above, i.e., narrower and straighter at the margins forewing orange bands with less hyalinity; **75.3.3.** The neotype specimen is a male bearing two white labels (1st handwritten on glassine paper, 2nd printed): [Guyana Iracoubo | Rocoucoua | III.85], [DNA sample ID: | NVG-18038E04 | c/o Nick V. Grishin], and shown in Fig. 33c; the neotype has a chipped inner margin of the right hindwing in the middle and its right antenna points more anteriad rather than along the costal margin of the forewing; **75.3.4.** We failed to find the lectotype of *P. aeacus* among Hesperiidae holdings in all collections we visited (see Acknowledgments for their list and see above) and catalogs we searched and believe that it was lost; **75.3.5.** The neotype closely agrees with the illustration of the *P. aeacus* lectotype in all characters, as evidenced by comparing the neotype shown in Fig. 33c with the illustration on pl. 75, fig. 2 in Swainson (1831) and the characters for this taxon listed above (75.3.2.); **75.3.6.** The neotype is from French Guiana and the original type locality "South America" agrees with it, as this phenotype is found mostly in the Amazonian region; **75.3.7.** The neotype is in the Senckenberg Naturmuseum, Frankfurt, Germany (SMF). As a result of the neotype designation, the type locality of *P. aeacus* becomes French Guiana: Iracoubo, Rococoua. The COI barcode sequence of the neotype, sample NVG-18038E04, GenBank PV549992, 658 base pairs, is:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTGGGAGCCCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTCTACCCCCCCTCTATCTGCCAATATTGC
CCATCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCCGTATTAGCAGGCGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCCGCAGGAGGGGGGGATCCTATTCTTTATCAACACTTATTT

Entheus guyaneus Grishin, new species

http://zoobank.org/630FF944-AA31-4407-A16A-9193FCA95218

(Figs. 31–32 part, 35, 36a–d, 50 part, 51e–f)

Definition and diagnosis. As detailed above, specimens from the Guianas that we initially identified as *Entheus priassus* (Linnaeus, 1758) (type locality in Suriname) partition into three species: *E. priassus*, *Entheus talaus* (Linnaeus, 1763), **stat. rest.** (type locality in the Amazonian region), and a new one, genetically differentiated from the others (Figs. 31–32); e.g., its COI barcodes differ by 0.6% (4 bp, the difference is small likely due to introgression of the COI barcode haplotype, similar in several species: Figs. 31b, 32b) from *E. priassus*, and by 1.8% (12 bp, a difference large for *Entheus*) from *E. talaus*. This new species keys to "*Entheus priassus priassus*" (B.10.4(a)) in Evans (1952) but differs from its relatives by a combination of the following characters: the doublet of semi-hyaline spots in the forewing cells M_1-M_2 and M_2-M_3 is stronger offset distad from the triplet of the subapical spots and is much narrower in a female; the semi-hyaline spot in the cell M_3-CuA_1 is connected to the discal orange band with a narrower link (i.e., the spot is constricted before the discal band) in males, and is narrower in females and closer to the submarginal doublet of spots than to the spot in the cell CuA_1-CuA_2; in males: the forewing discal orange band is typically narrower than in *E. priassus*, rather straight at the margins, with more limited hyaline areas distad, the hindwing is entirely dark brown on both sides, the hindtibial brush and tuft are orange-yellow; in a female: the hindwing white area above is larger than in *E. priassus*, the forewing semi-hyaline spots are smaller than in *E. talaus*, the spot in the cell CuA_1-CuA_2 is slightly offset distad from the discal cell spot, and there is no pale spot in the cell CuA_2-1A+2A by the vein 1A+2A. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly3824.1.21:T174C, aly3824.1.21:G180C, aly1042.23.1:C57T, aly1042.23.1:T78C, aly164.77.2:G24A; and COI barcode: C124C, 367T, T565C, T619T, A625G, T643C.

Barcode sequence of the holotype. Sample NVG-14062D01, GenBank PV549993, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTGGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCATCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCCGTATTAGCAGGCGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGGGGAGGAGATCCTATTCTCTATCAACACTTATTT

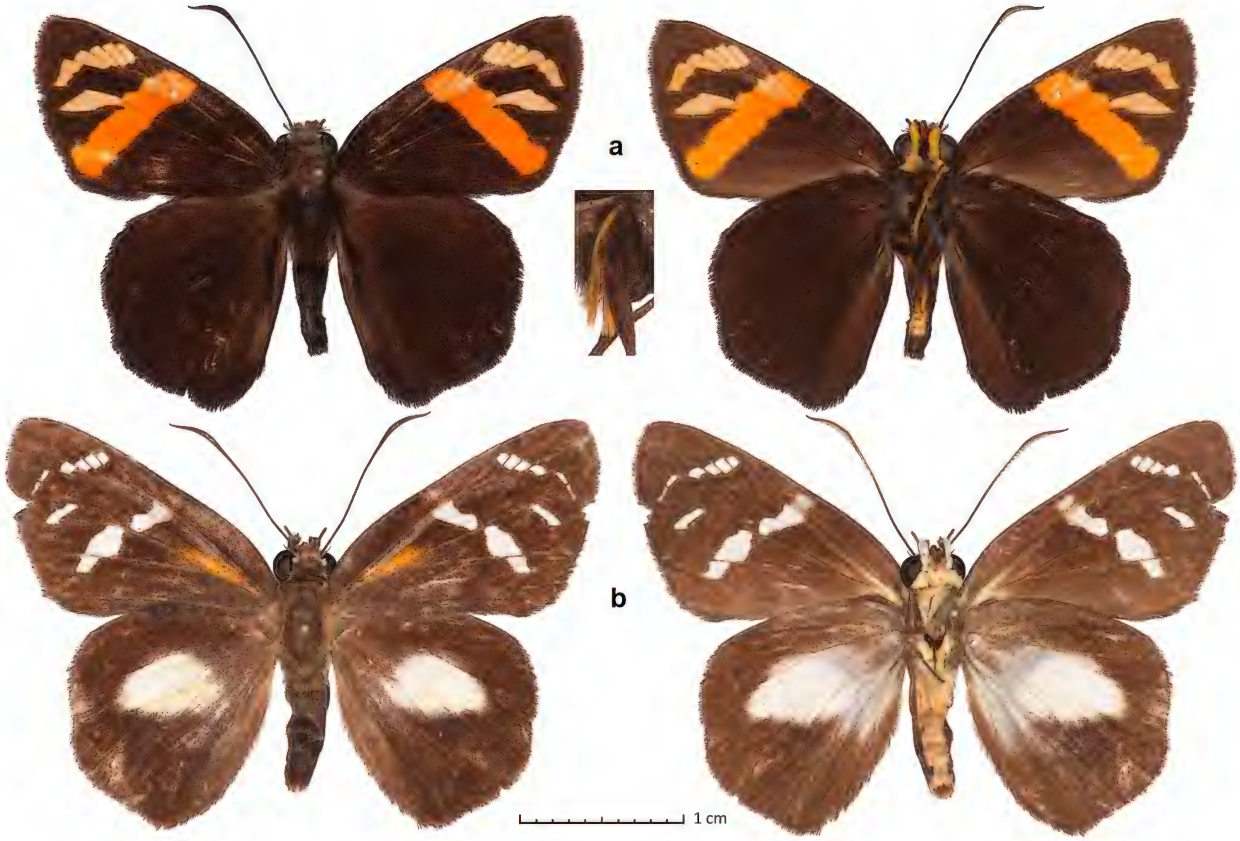


Fig. 35. *Entheus guyaneus* **sp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-14062D01, inset shows hindtibial tuft enlarged two times compared to specimens (scale not given); **b)** paratype ♀ NVG-14062D05.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Figs. 35a and 51e (genitalia Fig. 36a–d), bears the following six printed rectangular labels, five white: [GUYANA: Cuyuni R, | Kamaria Falls 100' | 30.XI.-5.XII.2000 | 6°24'N 58°546'W | Leg. S.Fratello et al], [DNA sample ID: | NVG-14062D01 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119D12 | c/o Nick V. Grishin], [genitalia: | NVG240817-39 | c/o Nick V. Grishin], [{QR Code} | USNM ENT 00179768], and one red [HOLOTYPE ♂ | Entheus | guyaneus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratypes:** 1♂ and 2♀♀ with the same data as the holotype except as indicated: 1♂ NVG-14062C05 USNM ENT 00179818, 1♀ NVG-14062D05 USNM ENT 00275189, and 1♀ NVG-23112G08 Kartabo, 10-Jul-1925, G. D. Morgan leg. [CMNH].

Type locality. Guyana: Cuyuni-Mazaruni Region, Cuyuni River, Kamaria Falls, approx. GPS 6.40, −58.77.

Etymology. The name is formed from the name of the country with the type locality and is treated as a masculine noun in apposition.

Distribution. Currently known only from north-central Guyana (Cuyuni-Mazaruni Region).

Entheus colombeus Grishin, new species

http://zoobank.org/CE830AFA-9AE0-4B04-A57B-7C81ECDAECBE

(Figs. 31 part, 37–38, 50 part, 51h)

Definition and diagnosis. Genomic analysis of *Entheus* Hübner, [1819] (type species *Papilio peleus* Linnaeus, 1763, which is a junior subjective synonym of *Papilio priassus* Linnaeus, 1758) reveals that a

Fig. 36. Male genitalia of *Entheus* holotypes (unless indicated), data in text: **a–d)** *E. guyaneus* NVG-23119D12; **e–g)** *E. proxemus* NVG-24064A01; **h–k)** *E. peruveus* NVG-23119E01; **l–o)** *E. pano* NVG-23119E02; **p–w)** *E. venezuelius* NVG-15026F10; **x–z)** *E. venezuelius* paratype NVG-24028H11 in different views: **a**, **e**, **h**, **l**, **s**, **u**, **w**, **x)** left lateral; **b**, **f**, **i**, **m**, **p**, **v**, **y)** dorsal; **c**, **j**, **n)** posteroventral; **d**, **g**, **k**, **o**, **r**, **z)** posterior; **q)** ventral; **t)** right lateral. Complete genital capsule is shown, except **p–s)** with **u**, **v)** right and **w)** left valvae and **t)** aedeagus detached. Panel letters are on the lower right of each image.

Fig. 37. *Entheus colombeus* **sp. n.** holotype ♂ NVG-15099C09 in dorsal (left) and ventral (right) views, data in text. The inset shows the hindtibial tuft enlarged two times compared to the specimen (scale not given).

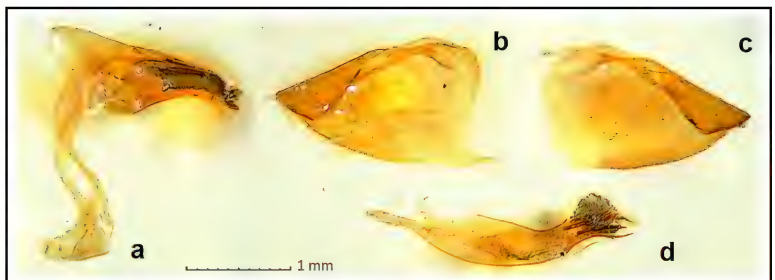


Fig. 38. Genitalia of *Entheus colombeus* **sp. n.** holotype ♂, slide 483 (views): **a)** genitalia with valvae and aedeagus detached (left lateral); **b)** left valva (right lateral); **c)** right valva (left lateral); **d)** aedeagus (left lateral). Dorsal tips of both harpes folded over during the slide mount.

male from eastern Colombia does not group with any single known species with strong statistical support (65% with *Entheus curvus* Austin, 1997 in the nuclear genome tree of this group, Fig. 31a, and 87% within the *E. telemus* subgroup in the *Entheus* species tree, Fig. 50a) and is genetically differentiated from them at the species level in the nuclear genome (Fig. 31a). However, likely due to introgression, the COI barcode of this Colombian specimen is shared with *Entheus priassus* (Linnaeus, 1758) (type locality stated in Suriname) and *Entheus curvus* Austin, 1997 (type locality in Peru: Loreto), although the overall mitochondrial genome differentiates them (Fig. 31b). Due to its genetic differentiation and phylogenetic position in the nuclear genome tree, this specimen represents a new species. This new species keys to "*Entheus priassus telemus*" (B.10.4(b)) in Evans (1952) and is phenotypically closer to *Entheus latebrosus* Austin, 1997 (type locality Ecuador: Limoncocha, Río Napo), *Entheus telemus* Mabille, 1898 (type locality in Brazil) and the next two new species described below, but differs from them by a combination of the following characters in males (female unknown): forewing orange spotting is intermediate in width and extent between *Entheus telemus* Mabille, 1898 (type locality in Brazil) and *E. priassus*: color is yellower than in *E. telemus*, the subapical band is narrowly connected with the discal band at the anterior distal end of the discal cell leaving a brown triangle towards the costa, the spot between the bands is not engulfed by the posterior segment of the discal band (engulfed in *E. telemus*) and the outer margin of the discal band is straight and aligned anterior and posterior of the middle spot; the hindwing is entirely dark brown on both sides; the hindtibial brush is orange and the tuft is brown, darker than in *E. priassus* but paler than in *E. telemus*. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly669.15.1: C1056T, aly669.15.1:A1089C, aly4456.7.2:A78T, aly4456.7.2:G102T, aly727.9.9:G183A, aly3404.1.20: G159G (not A), aly3404.1.20:G162G (not A), aly3404.1.20:A169A (not T), aly2835.2.15:C96C (not A), aly2835.2.15:C102C (not T). This species cannot be confidently identified by the COI barcode (possibly due to introgression), while differing from related species in other regions of the mitochondrial genome (Fig. 31b, 50c).

Barcode sequence of the holotype. Sample NVG-15099C09, GenBank PV549994, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACTGCGCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTGGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCCGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTCTTTATCAACACTTATTT

Type material. Holotype: ♂ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Figs. 37 and 51h (genitalia Fig. 38), bears the following six printed (text in italics handwritten) rectangular labels, five white: [East Colombia], [734], [Genitalia Slide | No. *483*], [Exch. A.N.S.P. | C.M.Acc.20359], [DNA sample ID: | NVG-15099C09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | colombeus Grishin].

Type locality. Eastern Colombia.

Etymology. The name is formed from the type locality and is treated as a masculine noun in apposition.

Distribution. Currently known only from the holotype collected in eastern Colombia.

Comment. We have not attempted to remount the old genitalia slide No. 438 (currently in the CMNH cabinet with genitalia slides, mostly prepared by R. Williams) and illustrate genitalia here in their original condition, as mounted with dorsal tips of both harpes folded over, likely during the slide preparation (Fig. 38). The harpes are three-dimensional and smoothly curve inward (towards each other), creating a challenge with mounting on a flattened slide.

Entheus proxemus Grishin, new species

http://zoobank.org/4EE1D5A2-1A38-4181-92C5-41E59B1C5AB2

(Figs. 31 part, 36e–g, 39, 50 part, 51i)

Definition and diagnosis. Genomic analysis of *Entheus* Hübner, [1819] (type species *Papilio peleus* Linnaeus, 1763, which is a junior subjective synonym of *Papilio priassus* Linnaeus, 1758) reveals that a male from Pará, Brazil, is sister to *Entheus telemus* Mabille, 1898 (type locality in Brazil), but is genetically differentiated from it at the species level (Figs. 31, 50); e.g., their COI barcodes differ by 1.5% (10 bp, a difference large for *Entheus*), thus representing a new species. This new species keys to "*Entheus priassus telemus*" (B.10.4(b)) in Evans (1952) but differs from its relatives by a combination of the following characters in males (female unknown): forewing bands are yellower (not intensely orange as in *E. telemus*), especially the subapical band and the spot between the bands, and narrower, i.e., the distal and basal margins of the discal band are more straight, the distal margin is not engulfing half of the posterior margin of the spot between the bands; the subapical band is broadly connected with the discal band from the anterior end of the discal cell towards the costa; the hindwing is entirely dark brown on both sides. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly2487.1.3:G54A, aly2487.1.3:T63C, aly127.63.3:T1122C, aly3319.1.10:A153G, aly1042.29.12:A108C, aly2954.6.6:T306T (not C), aly26.15.3:A48A (not T), aly363.10.3:A258A (not T), aly7917.5.6:T384T (not C), aly1036.5.1:A807A (not T); and COI barcode: A28A, T127T, C367T, G506A, 526C, A562G.

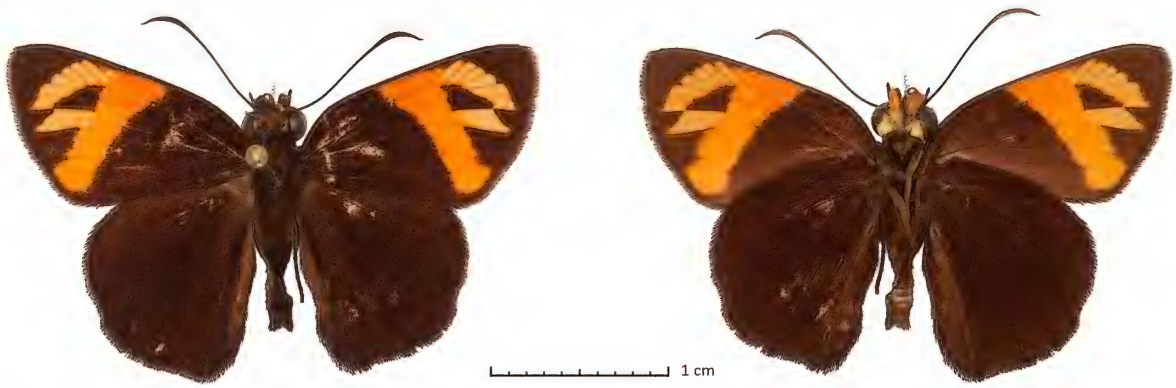


Fig. 39. *Entheus proxemus* **sp. n.** holotype ♂ NVG-23064B05 in dorsal (left) and ventral (right) views, data in text.

Barcode sequence of the holotype. Sample NVG-23064B05, GenBank PV549995, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCATCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTATTTGAGCAGTAGGTATTACCGCATTACTTTTATTATTATCTTTACCTGTATTAGCGGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCTATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Figs. 39 and 51i (genitalia Fig. 36e–g), bears the following seven printed rectangular labels, six white: [Belém, Pará | Brazil | January 11, 1961 | D.L.Lindsley], [Entheus Hübner | priassus (Linnaeus) | telemus Mabille], [D.L. Lindsley colln. | MGCL Accession | # 2008-20], [DNA sample ID: | NVG-23064B05 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24064A01 | c/o Nick V. Grishin], [genitalia: | NVG241111-01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | proxemus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Type locality. Brazil: Pará, Belém.

Etymology. The name is constructed as an antonym of its sister species' name, *telemus*. In Greek, τηλε- (*tele*-) is a prefix that means distant or far away. In Latin, *proximus* means nearest or next, and the name formed from this word is given to this species, nearest to *E. telemus*, with the distribution next to it. The name is treated as a masculine noun in apposition.

Distribution. Currently known only from the holotype collected in the lower Amazonian region.

Entheus peruveus Grishin, new species

http://zoobank.org/8C6657DF-7D8B-4BF8-B177-F17E64A7C11F

(Figs. 31 part, 36h–k, 40, 50 part, 51j–k)

Definition and diagnosis. Genomic analysis reveals a clade of specimens from Peru that is sister to *Entheus latebrosus* Austin, 1997 (type locality in Ecuador, holotype sequenced as NVG-15021E04) in the nuclear genome tree but is in a different clade from *E. latebrosus* in the mitochondrial genome tree, suggesting that it represents a new species due to its inconsistent phylogenetic position and genetic differentiation (Figs. 31, 50), e.g., its COI barcodes differ from *E. latebrosus* by 2.0% (13 bp). This new species keys to "*Entheus priassus telemus*" (B.10.4(b)) in Evans (1952) but differs from its relatives by a combination of the following characters: in males, forewing bands are bright-orange, the discal band without hyaline areas, the spot between the bands with only a hint of hyalinity distally, and the anterior four spots of the subapical band are semi-hyaline, the posterior two spots mostly opaque and are moderately (by a third to a half of the spot width) offset distad from the anterior three spots; the subapical band is not connected to the discal band; the hindwing is uniformly dark brown on both sides, the hindtibial tuft is tawny; in a female, hyaline and white spots are larger than in *E. latebrosus*, forewing subapical spots form a continuous band, with the two posterior spots offset distad, discal spots broader, the spot in cell M_3-CuA_1 is slightly closer to the spot in the cell CuA_1-CuA_2 than in the cell M_2-M_3, the dorsal hindwing white area is rectangular, reaching the inner margin, and the brown marginal area is narrower than the white area. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly3839.2.5:C114T, aly3839.2.5:C144T, aly3712.5.7:G120T, aly113.12.1: C94T, aly113.12.1:G111A; and COI barcode: T115C, A133G, A433G, T526C, T610C.

Barcode sequence of the holotype. Sample NVG-14062B08, GenBank PV549996, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTACAATACT
ATTGTTACTGCGCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGGGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACCGCATTACTTTTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTCTTTGATCCTGCAGGAGGAGGAGATCCTATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Figs. 40a and 51k (genitalia Fig. 36h–k), bears the following five printed (text in italics handwritten) rectangular labels, four white: [PERU Madre De

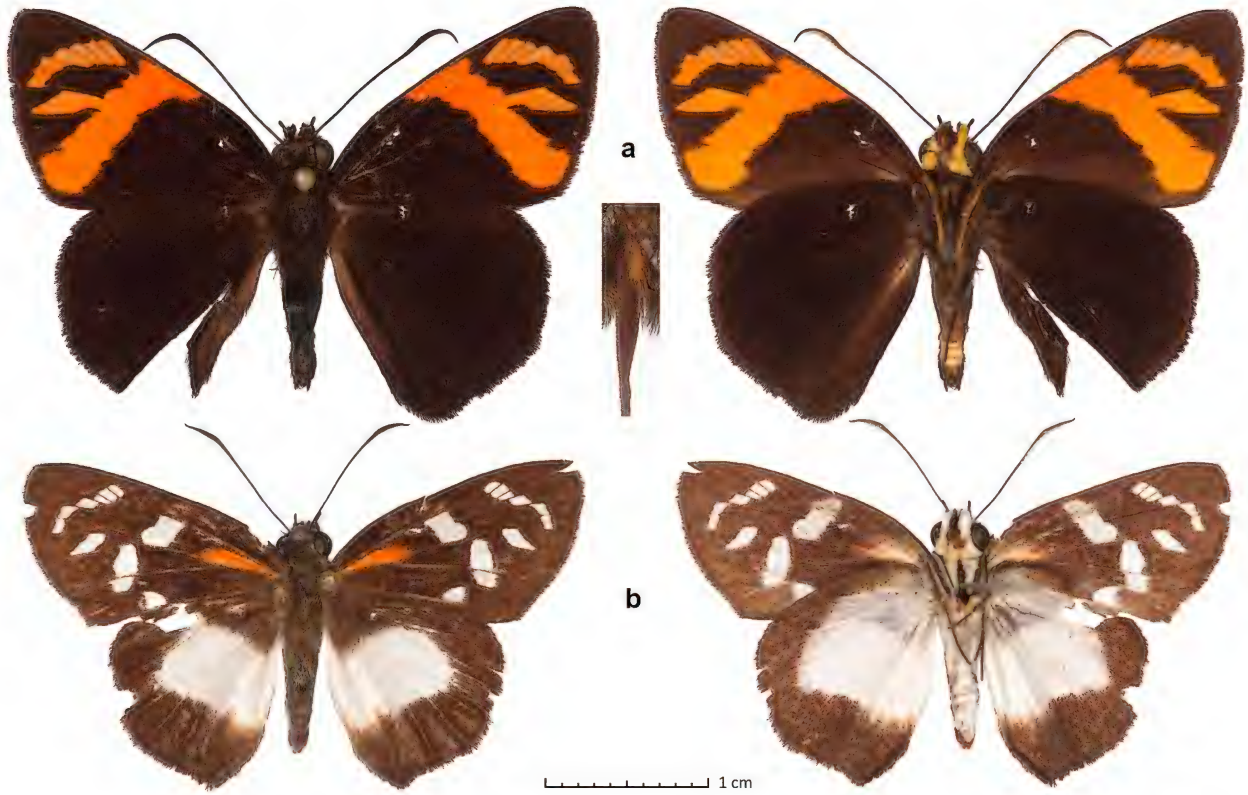


Fig. 40. *Entheus peruveus* **sp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-14062B08, inset shows hindtibial tuft enlarged two times compared to specimens (scale not given); **b)** paratype ♀ NVG-14062B03.

Dios | Rio La Torre 300m | Tambopata Res. | *31 Oct.'84* | S. S. Nicolay], [DNA sample ID: | NVG-14062B08 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E01 | c/o Nick V. Grishin], [genitalia: | NVG240817-40 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | peruveus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratypes:** 3♂♂ and 1♀ from Peru, Madre de Dios: 1♂ NVG-23116H05 data as the holotype but 6-Oct-1986, D. H. Ahrenholz leg.; 1♂ NVG-23064B06 near the type locality, given as Rio Tambopata, 60 km S Puerto Maldonado, Rio Tambopata, 60 km S Puerto Maldonado, D. & J. Lindsley leg. [MGCL]; 1♂ NVG-23116H04 30 km SW Pto. Maldonado, 300 m, 20-Oct-1983, S. S. Nicolay leg. [USNM]; and 1♀ NVG-14062B03 Manu National Park, Pakitza, −12.1167, −70.9667, 16-Sep-1989, D. J. Harvey leg. [USNM] (Figs.40b, 51j).

Type locality. Peru: Madre de Dios Region, Tambopata National Reserve, Rio La Torre, elevation 300 m.

Etymology. The name is formed from the name of the country with the type locality and is treated as a masculine noun in apposition.

Distribution. Currently known from southeastern Peru.

Entheus hyponota Grishin, new species

http://zoobank.org/88821A37-2D04-4B28-9571-10216DE05D49

(Figs. 31 part, 34d–f, 41, 50 part, 51l)

Definition and diagnosis. Genomic analysis of the female specimen illustrated by Staudinger (1884–1888) as a "male" (a lapsus on the plate but not in the text) of "*Entheus talaus*" (Linnaeus, 1763) reveals that it is sister to *Entheus aureanota* Austin, O. Mielke & Steinhauser, 1997 (type locality in Brazil: Rondônia), but is genetically differentiated from it at the species level (Figs. 31, 50): e.g., their COI barcodes differ by 2.1% (14 bp), thus representing a new species. This new species keys to "*Entheus*

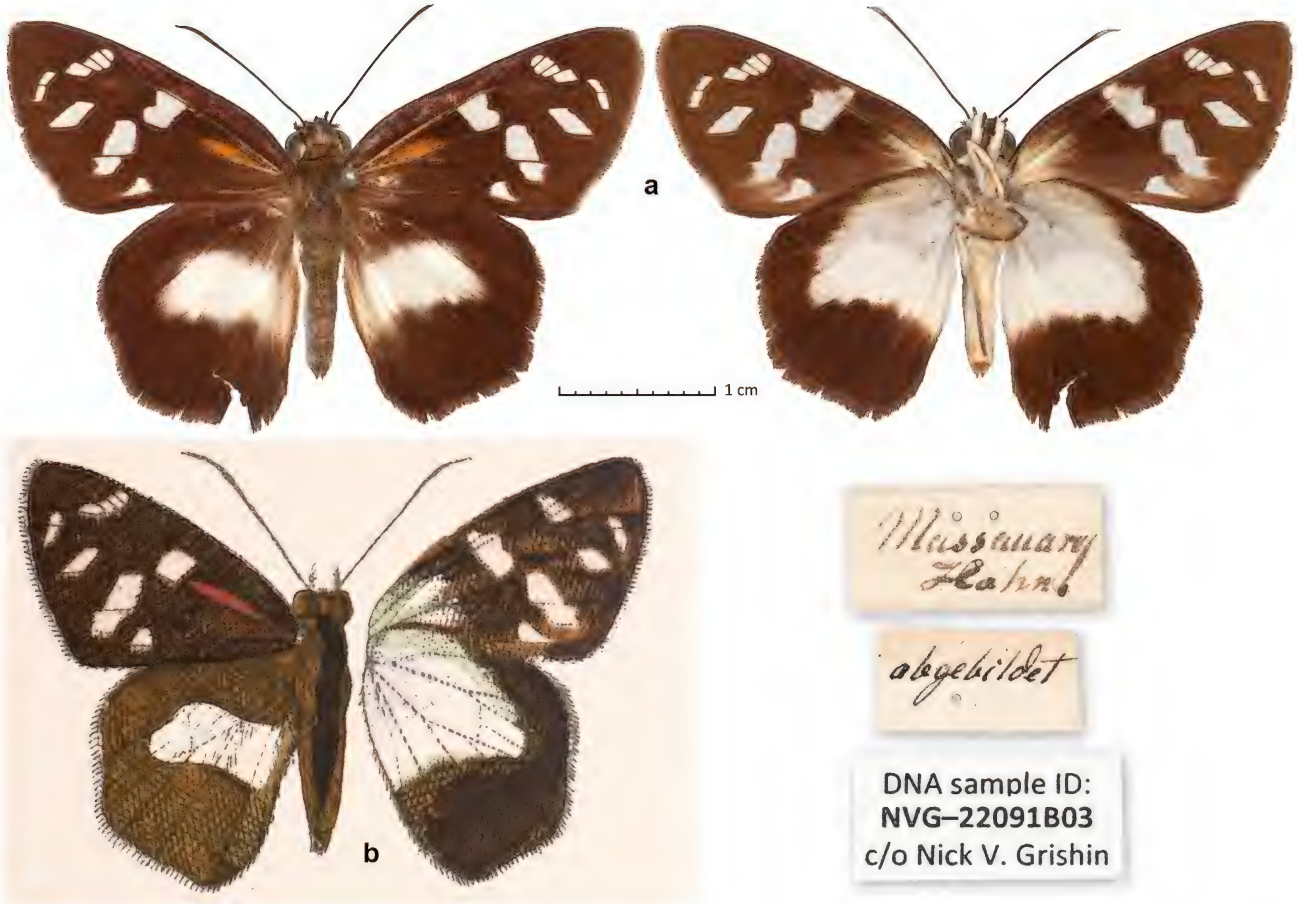


Fig. 41. *Entheus hyponota* **sp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♀ NVG-22091B03 with its labels below on the right and **b)** its illustration from Staudinger (1884–1888), identified as *E. talaus* at the time.

priassus telemus" (B.10.4(b)) in Evans (1952) but differs from its relatives by a combination of the following characters in a female (male unknown): the hindwing white area reaching the inner margin where it is overscaled with brown, dorsally about half of the white area size in *E. aureanota*, occupying less than half of the wing and the brown part of the wing towards the outer margin is wider than the white area; the subapical semi-hyaline forewing band is broken with the two posterior spots (submarginal doublet) offset distad from the rest (all spots are aligned in *E. pralina*); the white spot by the forewing vein 1A+2A is slightly smaller than the spot posterior to the vein CuA_2. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1313.35.3:G72A, aly1313.35.3:T75G, aly5294.28.5:C45G, aly5294.28.5:T75G, aly5543.1.4:G12C, aly2668.6.1:G252G (not C), aly2668.6.1:C273C (not T), aly256.9.3:T732T (not A), aly128.15.1:A729A (not G), aly1863.15.1:G207G (not A); and COI barcode: T115C, 124C, A181G, T508C, A517G, T596C, T601C.

Barcode sequence of the holotype. Sample NVG-22091B03, GenBank PV549997, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTACAATACT
ATCGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGGGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATCACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTCTGAGCAGTGGGTATTACTGCATTACTTTTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATCTAAACACAT
CATTTTTTGATCCTGCGGGAGGAGGAGATCCTATTCTTTATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Figs. 41 and 511 (genitalia Fig. 34d–f), bears the following six rectangular labels (first two handwritten, others printed), five white: [Massauary | Hahn.], [abgebildet], [DNA sample ID: | NVG-22091B03 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24029A08 | c/o Nick V. Grishin], [genitalia: | NVG241114-19 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Entheus | hyponota

Grishin]. It was collected by Paul Hahnel and illustrated in Staudinger (1884–1888). The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Type locality. Brazil: Amazonas, Massauari.

Etymology. The name is given to rhyme with its sister species *E. aureanota*, replacing *aureo-* with *hypo-* (in Greek, meaning under- or below, and *-nota* meaning mark or spot in Latin) for the underdeveloped white region on the dorsal hindwing compared to its sister. The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in the middle Amazonian region in Brazil.

Entheus pralina Evans, 1952 is a species distinct from *Entheus priassus* (Linnaeus, 1758)

Genomic analysis reveals that *Entheus priassus pralina* Evans, 1952 (type locality in Brazil: Espirito Santo) is not sister to and genetically differentiated from *Entheus priassus* (Linnaeus, 1758) (type locality in Suriname) at the species level (Figs. 31, 50); e.g., their COI barcodes differ by 1.4% (9 bp). This is a comparatively large COI difference for *Entheus*, e.g., COI barcodes of *E. priassus* and *Entheus curvus* Austin, 1997 (type locality in Peru: Loreto) differ by 0.6% (4 bp). Therefore, we propose that *Entheus pralina* Evans, 1952, **stat. nov.** is a species distinct from *Entheus priassus* (Linnaeus, 1758).

Entheus lina Grishin, new species

http://zoobank.org/CB2B2C09-31DE-4656-A791-D3DFFDCA9A46

(Figs. 31 part, 34g–i, 42, 50 part, 51g)

Definition and diagnosis. Genomic analysis reveals that a female from Brazil (either Bahia or Pará) is sister to *Entheus pralina* Evans, 1952, **stat. nov.** (type locality in Brazil: Espírito Santo) and is genetically differentiated from it at the species level (Figs. 31, 50). e.g., their COI barcodes differ by 0.8% (5 bp), thus representing a new species. This new species keys to "*Entheus priassus telemus*" (B.10.4(b)) in Evans (1952) but differs from its relatives by a combination of the following characters in a female (no males known): the subapical hyaline forewing band is broken with the two posterior spots (submarginal doublet) offset distad from the rest (all spots are aligned in *E. pralina*); the hindwing white area is larger than in relatives, reaching the inner margin, with a concave and wavy distal margin and brown scales reach into it along veins, and the boundary between the white area and brown postdiscal part of the wing is blurred towards the inner wing margin; the white spot by the forewing vein 1A+2A is slightly smaller than the spot posterior to the vein CuA_2. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly481.27.16:G72A, aly481.27.16:A78G, aly536.13.5:T48C, aly2.1.14:C45T, aly26.33.23:T94C, aly113.11.15:T112T (not C), aly1196.8.8:C192C (not G), aly4003.1.4: C195C (not G), aly2706.1.2:C105C (not A); and COI barcode: 499T, T500T, T530C, 622A, A628G.

Fig. 42. *Entheus lina* **sp. n.** holotype ♀ NVG-15032C12 in dorsal (left) and ventral (right) views, data in text.

Barcode sequence of the holotype. Sample NVG-15032C12, GenBank PV549998, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGAACTTCCTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATCGTTACTGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTCTTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACTGTTTACCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCTGTAGATTTAGCCATTTTTTCCCTTCATTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTCTATTTGTTTGAGCAGTAGGTATTACTGCACTACTTTTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGGGGAGATCCTATTCTTTATCAACACTTATTT

Type material. Holotype: ♀ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Figs. 42 and 51g (genitalia Fig. 34g–i), bears the following seven rectangular labels (2nd and 3rd handwritten, others printed, 2nd bluish green, last red, and others white): [5146], [Talaus | Lin. Cl. Ic. 45. f.1. | Cram.393.C. Fab. | Hüb. Lep. ex. Vol. II. | | Bah.Sello–Pará Sieb], [talaus | L. | (priassus | L. | phereclus | L. | peleus Cl.)], [DNA sample ID: | NVG-15032C12 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24028H12 | c/o Nick V. Grishin], [genitalia: | NVG241114-18 | c/o Nick V. Grishin], and [HOLOTYPE ♀ | Entheus | lina Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. The holotype is one of four specimens in the lot number 5146, per the historical collection catalog, and was collected in Brazil either in Bahia by Friedrich Sello[w] or Pará by Friedrich Wilhelm Sieber. Considering substantial genetic differentiation between this new species and *E. pralina* from southern Brazil, we hypothesize that the holotype was collected in Pará.

Type locality. Brazil: Pará.

Etymology. The name is the last two syllables of the name of its sister species, shortened to indicate the more northern distribution of this species. The name is a noun in apposition.

Distribution. Currently known only from the holotype collected in Brazil, likely Pará.

Lectotype designation for *Entheus matho* Godman & Salvin, 1879

Entheus matho Godman & Salvin, 1879 was described on the basis of several specimens from Guatemala: Choctum (a small settlement Choctun in Alta Verapaz Department approx. GPS 15.67, −90.42 according to Selander and Vaurie (1962), one specimen from this locality, as deduced from the text in Godman and Salvin (1894)) and Nicaragua: Chontales (several specimens) (Godman and Salvin 1879). A specimen from Guatemala: Alta Verapaz, Senahú (approx. GPS 15.43, −89.90 according to Selander and Vaurie (1962)) was illustrated by Godman and Salvin (1894) after the original description of *E. matho*, but it is not a syntype, because it is not from the type locality. Notably, both localities in Guatemala (Senahú and Choctum) are mentioned in Godman and Salvin (1894), but only one (Choctum) bears a superscript '1' after the authors' names, referencing the original description (as the locality in Nicaragua after the collector's name). This mention of the two Guatemalan localities and a particular way of referencing by the superscript (Senahú is not referring to the original description) supports the conclusion that the specimen from Senahú is not a syntype. Notably, this specimen is not conspecific with most other specimens in the type series, which has led to confusion in the literature. For instance, Steinhauser (1989) misidentified "*matho*" and attributed this name to a species represented by this non-syntypic male from Senahú and illustrated in Godman &

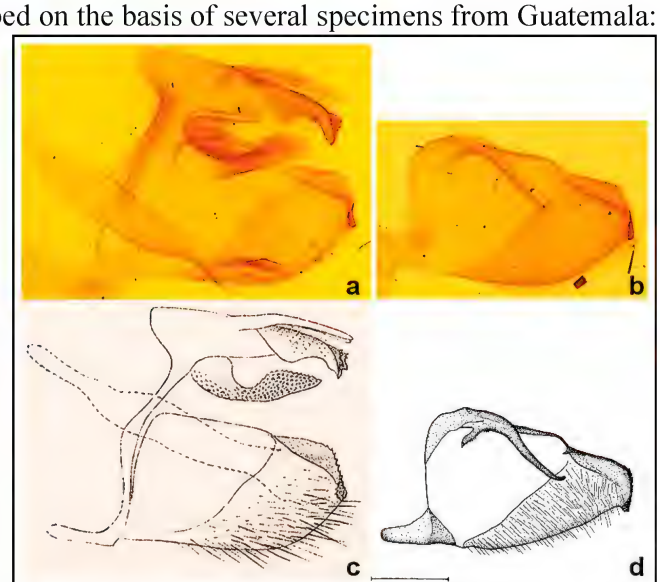


Fig. 43. Male genitalia of *Entheus*: **a–c)** *E. matho* lectotype minislide 108: **a)** genitalia with left valva detached; **b)** left valva, flipped (left-right inverted to facilitate comparison), interior view; **c)** illustration: fig. 29 on pl. 81 from Godman & Salvin (1894); **d)** *E. guato* **sp. n.** right valva, fig. 67 from Steinhauser (1989). **a**, **b)** © The Trustees of the Natural History Museum London and are made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/).

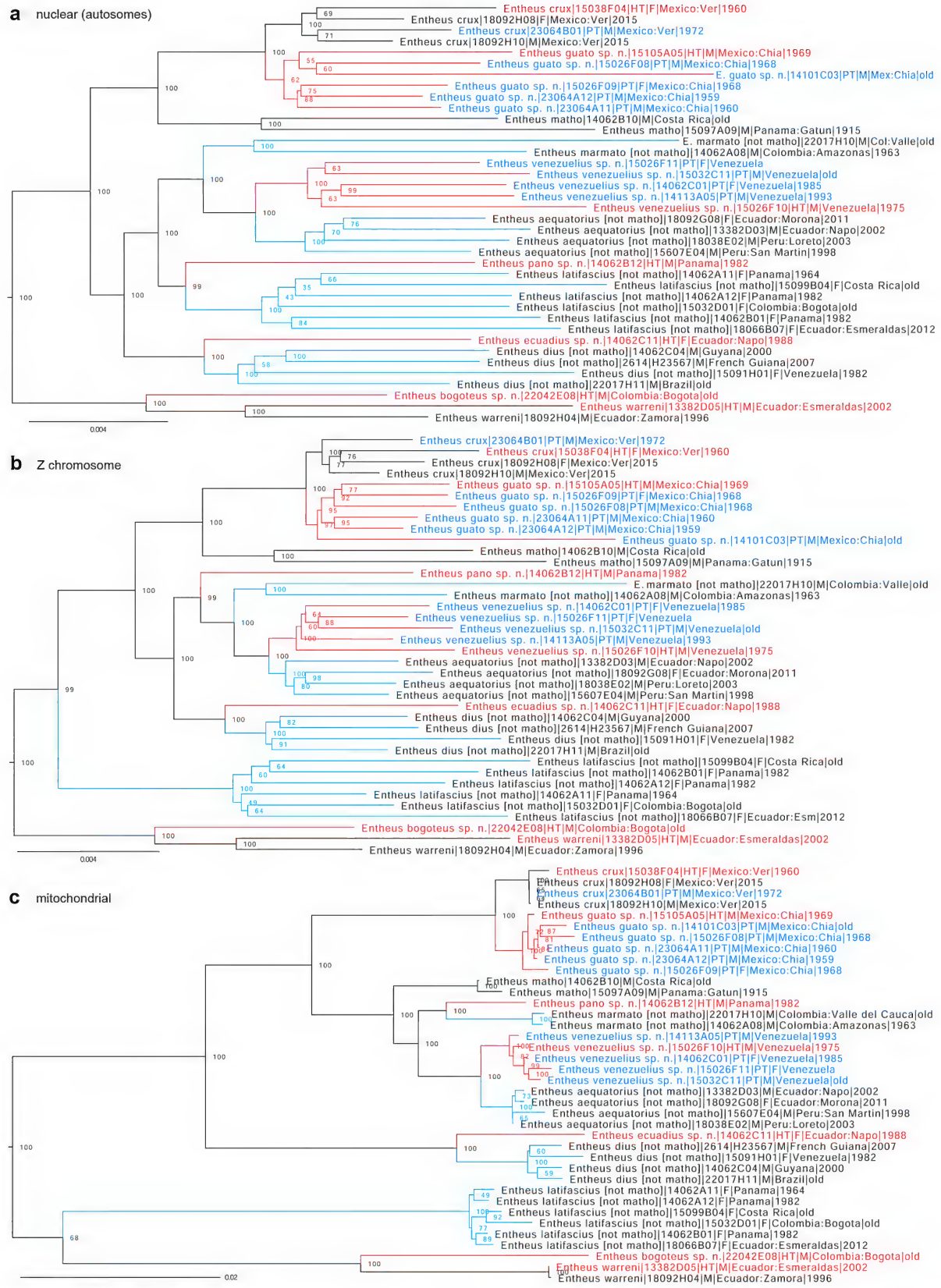


Fig. 44. Phylogenetic trees of *Entheus matho* group species inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,354,638 positions, **b)** the Z chromosome, based on 243,684 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Primary and secondary type specimens are labeled in red and blue, respectively. Branches of new taxa are shown in red and those with subspecies-to-species status change in blue.

Salvin (1894: pl. 81, fig. 28). In addition to the spread specimen, Godman & Salvin (1894: pl. 81, fig. 29) also illustrated the genitalia (reproduced here as Fig. 43c) of a syntype (Fig. 43a, b), and male genitalia can be used to identify *E. matho*, differing from other species by a wider harpe with a strongly convex ventral margin.

To stabilize nomenclature and define the name *E. matho* objectively in the light of confusion with the published misidentified illustration of its spread male that is not a syntype, N.V.G. hereby designates a syntype in the BMNH collection, a male with genitalia illustrated by Godman and Salvin (1894), that bears the following four rectangular printed labels and a genitalia minislide No. 108 pinned together with labels: [Chontales, | Nicaragua. | T. Belt.], [B.C.A.Lep.Rhop. | Entheus | matho, | G.&S.], [Godman-Salvin | Coll. 1912.—23.], [BMNH(E) #1054270] as the **lectotype** of *Entheus matho* Godman & Salvin, 1879. The lectotype has scales completely removed from its left wings to reveal venation and has the right forewing tornus chipped away. Images of this specimen are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *E. matho* becomes Nicaragua: Chontales. As a result, the species that Steinhauser (1989) misidentified as "*matho*" does not have a name and is new, described below.

Entheus guato Grishin, new species

http://zoobank.org/27E9B5AA-849F-4216-9962-841BA9008949

(Figs. 43d, 44 part, 45, 50 part, 51m)

Definition and diagnosis. Based on an illustration of a spread non-syntypic specimen in Godman and Salvin (1894), Steinhauser (1989) identified specimens from southeastern Chiapas, Mexico (near the border with Guatemala) as *Entheus matho* Godman & Salvin, 1879 (type locality in Nicaragua: Chontales), as discussed above. According to the taxonomic identity of the *E. matho* lectotype designated above, these specimens are not conspecific with *E. matho* and represent a new species. This species is sister to *Entheus crux* Steinhauser, 1989 (Veracruz, Mexico: Veracruz, Catemaco) and is more genetically distant from *E. matho* (Figs. 44, 50), e.g., its COI barcodes differ by 0.9% (6 bp) from *E. crux* and by 2.9% (19 bp) from *E. matho*. The description and diagnosis for this new species were given by Steinhauser (1989) for *E. matho*, because Steinhauser's *E. matho* is simply this new species, which he misidentified. In particular, Steinhauser (1989) differentiated it from his newly described *E. crux*, illustrating male and female genitalia of both species. This new species differs from both *E. matho* and *E. crux* by a narrower harpe with a straighter ventral margin (Fig. 43d), but the harpe is much broader with its ventral margin convex in *E. matho* (Fig. 43a–c). In facies, males of this new species differ from its relatives by more extensive red overscaling above, frequently with a well-developed reddish arc from the base of the forewing discal cell (as in females); and by a straight and broad array of the subapical semi-hyaline amber spots with the two posterior spots not being offset distad along the inner margin of this

Fig. 45. *Entheus guato* **sp. n.** holotype ♂ NVG-15105A05 in dorsal (left) and ventral (right) views, data in text.

subapical band as in typical *E. matho*. The hindtibial tuft is tawny, approximately the same color as the reddish overscaling of the dorsal side. In DNA, a combination of the following base pairs is diagnostic in the nuclear genome: aly18826.3.2:A51T, aly18826.3.2:T90C, aly318.26.5:C150T, aly2627.18.2:C81T, aly5294.4.3:T120A; and COI barcode: 49T, T59T, T133C, T499C, A628G.

Barcode sequence of the holotype. Sample NVG-15105A05, GenBank PV549999, 658 base pairs:

AACTTTATATTTTATTTTCGGAATCTGAGCAGGAATAGTAGGTACTTCTTTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGGGGTTTTGGAAATTGACTAGTACCTTTAATATTGGGAGCCCCTGATATAGCTTTCCCTCGAA
TAAATAACATAAGTTTTTGACTTCTACCCCCATCATTAACATTGTTAATTTCTAGAAGAATTGTCGAAAATGGAGCTGGAACAGGATGAACAGTTTACCCCCCTTTATCTGCTAATATTGC
CCACCAAGGATCTTCAGTAGATTTAGCTATTTTCTCCCTTCATTTAGCTGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAACTTATCA
TTTGATCAAATACCCCTATTTGTTTGAGCAGTAGGTATTACCGCACTACTTTTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGGGGAGATCCAATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the collection of the California Academy of Sciences, San Francisco, CA, USA (CAS), illustrated in Figs. 45 and 51m, bears the following six printed (text in italics handwritten) rectangular labels, five white: [MEX., Chiapas, | 27 km. S.E. Sta. Rosa | June '69; P. Hubbell], [Collection of | C. D. MacNeill], [*Entheus matho* | *matho G.&S.* | Det. C.D. MacNeill *'87*], [ ] both antennae and a leg are glued to this label, no text, [DNA sample ID: | NVG-15105A05 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | guato Grishin]. **Paratypes:** 5♂♂ and 1♀: Mexico, Chiapas: 1♂ NVG-14101C03 no detailed locality, coll. Franck Johnson, genitalia slide G2176 [AMNH] and Comitán, Santa Rosa, T. Escalante leg. [MGCL]: 1♂ NVG-23064A12, Specimen no. 29216, Apr-1959, 1♂ NVG-23064A11, Specimen no. 29217, Feb-1960, 1♂ NVG-15026F08, Specimen no. 29215, Apr-1968, and 1♀ NVG-15026F09, Specimen no. 29220, Apr-1968, genitalia SRS-1211; and 1♂ BMNH(E) #1054213 Guatemala, Alta Verapaz Department, Senahú, Champion leg. [BMNH].

Type locality. Mexico: Chiapas, Comitán, 27 km southeast of Santa Rosa.

Etymology. The name is given for the locality of the specimen misidentified and illustrated by Godman and Salvin (1894) as *E. matho*. The name is treated as a masculine noun in apposition.

Distribution. Mexico: Chiapas (near the border with Guatemala) and Guatemala.

Comment. The specimen with better DNA preservation was selected as the holotype.

Entheus dius Mabille, 1898, *Entheus aequatorius* Mabille & Boullet, 1919, *Entheus latifascius* M. Hering, 1925, and *Entheus marmato* Salazar & Vargas, [2017], are species distinct from *Entheus matho* Godman & Salvin, 1879

Genomic analysis of the *Entheus matho* group reveals that *Entheus dius* Mabille, 1898 (type locality in Brazil), *Entheus aequatorius* Mabille & Boullet, 1919 (type locality given in the original description as "Bolivia" likely by mistake, and may be in Ecuador: Bolivar), *Entheus latifascius* M. Hering, 1925 (type locality Colombia, Chocó, Rio Micay), and *Entheus matho marmato* Salazar & Vargas, [2017] (type locality in Colombia: Caldas, Marmato-vereda Echandía) are not monophyletic and are genetically differentiated from *Entheus matho* Godman & Salvin, 1879 (type locality in Nicaragua: Chontales) and among each other at the species level (Figs. 44, 50): e.g., COI barcodes in the pairs of closest taxa differ by 1.5% (10 bp, *E. aequatorius* and *E. matho*), 1.7% (11 bp, *E. matho marmato* and *E. matho*), 2.3% (15 bp, *E. aequatorius* and *E. matho marmato*), but more distant from each other, *E. latifascius* and *E. dius* differ by 5.3% (35 bp). Therefore, instead of being subspecies of *E. matho* as currently considered, these four are species-level taxa: *Entheus dius* Mabille, 1898, **stat. rest.**, *Entheus aequatorius* Mabille & Boullet, 1919, **stat. rest.**, *Entheus latifascius* M. Hering, 1925, **stat. rest.**, and *Entheus marmato* Salazar & Vargas, [2017], **stat. nov**.

Entheus pano Grishin, new species

http://zoobank.org/3A566915-7C92-470F-816F-5063C76BC6A0

(Figs. 36l–o, 44 part, 46, 50 part, 51n)

Definition and diagnosis. Genomic analysis of *Entheus* Hübner, [1819] (type species *Papilio peleus* Linnaeus, 1763, which is a junior subjective synonym of *Papilio priassus* Linnaeus, 1758) reveals that a

specimen from Panama is genetically differentiated from all other described taxa in the *Entheus matho* group at the species level, and its phylogenetic position differs in the trees constructed from different genomic regions (autosomes, Z chromosome, mitochondrial genome), indicating complexities in the evolution of this lineage (Figs. 44, 50). Its COI barcode differs by 2.1% (14 bp) from *Entheus marmato* Salazar & Vargas, [2017], **stat. nov.** (type locality in Colombia: Caldas, Marmato-vereda Echandía), which is its sister in the mitochondrial genome tree (Figs. 44c, 50c). Therefore, this specimen represents a new species. This new species keys (incompletely) to "*Entheus matho matho*" (B.10.5(a)) in Evans (1952) and differs from its relatives by a combination of the following characters in males (female unknown): the forewing discal band is orange, semi-hyaline along parts of the distal margin, the apical band and the spot between the bands are semi-hyaline, orange-yellow, the spot is closer to the apical band than to the discal band, nearly rectangular, the two posterior spots of the apical band are offset by about their half-width distad from the rest at both margins of the band, the ground color is rusty brown, no basal reddish arc on the forewing, the anal fold is cream-white in the middle, slightly yellower towards its margins, and the hindtibial tuft is buff-tawny. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly54.45.5:C105T, aly54.45.5:C108T, aly54.45.5:C123A, aly994.10.10:G75A, aly1651.42.9:C204T, aly1260.25.9:A134A (not G), aly240.18.17:T36T (not C), aly240.18.17:G51G (not A), aly1968.11.2:G69G (not A), aly1968.11.2:T75T (not G); and COI barcode: C19T, A214G, C364T, C400T, T478C, T526C.

Barcode sequence of the holotype. Sample NVG-14062B12, GenBank PV550000, 658 base pairs:

AACTTTATATTTTATTTTTGGAATCTGAGCAGGAATAGTAGGTACTTCCCTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGTTTTGGAAATTGATTAGTACCTTTAATATTGGGAGCCCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACAGTTTACCCCCCTTTATCTGCTAATATTGC
TCATCAAGGATCTTCAGTAGATTTAGCTATTTTTTCTCTTCATTTAGCTGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAACTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACCGCACTACTTTTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGATCCAATTCTTTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Figs. 46 and 51n (genitalia Fig. 36l–o), bears the following five printed rectangular labels, four white: [PANAMA: Darien | Cana 1200m | 13.IX.1982 | Leg. G. B. Small], [DNA sample ID: | NVG-14062B12 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E02 | c/o Nick V. Grishin], [genitalia: | NVG240817-41 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | pano Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Type locality. Panama: Darién Province, Cana, elevation 1200 m.

Fig. 46. *Entheus pano* **sp. n.** holotype ♂ NVG-14062B12 in dorsal (left) and ventral (right) views, data in text. The inset shows the hindtibial tuft enlarged two times compared to the specimen (scale not given).

Etymology. The name is formed from the name of the country with the type locality to end in *-o* as *E. mato*. The name is treated as a masculine noun in apposition.

Distribution. Currently known only from the holotype collected in eastern Panama.

Entheus venezuelius Grishin, new species

http://zoobank.org/3DE8615E-5BAB-43AB-8EDD-DEA0B421FCF3

(Figs. 36p–z, 44 part, 47, 50 part, 51o–p)

Definition and diagnosis. Genomic analysis reveals that specimens from Venezuela that are traditionally identified as *Entheus aequatorius* Mabille & Boullet, 1919, **stat. rest.** (type locality given in the original description as "Bolivia" likely by mistake, and may be in Ecuador: Bolivar), are indeed its sister, but are genetically differentiated from it at the species level (Figs. 44, 50); e.g., their COI barcodes differ by 1.2% (8 bp), thus representing a new species. This new species keys to "*Entheus matho aequatorius*"(B.10.5(c)) in Evans (1952) who included it into this taxon, but noted that Venezuelan specimens were "smaller, ♀ upf with spot mid costa," and differs from its relatives by a combination of the following characters: smaller in size; males with more extensive rusty overscaling on both sides of the wings, the color of the forewing bands and spots is yellower, less orange; the tibial tuft is tawny, paler than in *E. aequatorius*; the pale area of the anal fold is smaller and yellower; females with a white area on the hindwing more restricted towards the anal margin and a pale spot by mid-costa on the forewing aligned with the discal cell white spot, not offset basad. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs

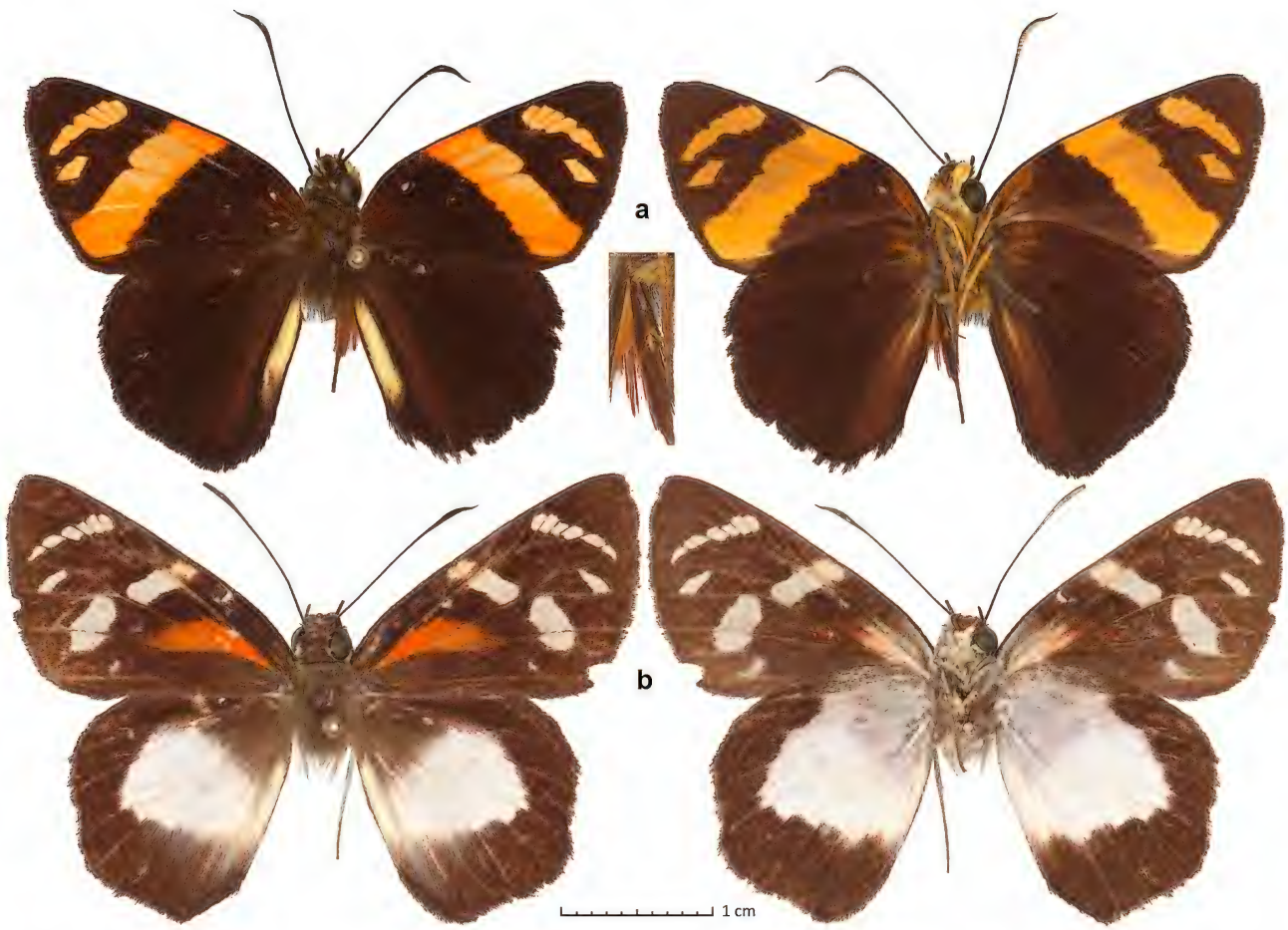


Fig. 47. *Entheus venezuelius* **sp. n.** in dorsal (left) and ventral (right) views, data in text: **a)** holotype ♂ NVG-15026F10, inset shows hindtibial tuft enlarged two times compared to specimens (scale not given) and **b)** paratype ♀ NVG-15026F11.

is diagnostic in the nuclear genome: aly2653.1.9:C117G, aly2130.3.5:T153C, aly997.1.7:T42A, aly671.50.4:C147T, aly2874.5.3:G177A; and COI barcode: T49C, T115C, T226C, A373G, G506G, T646C.

Barcode sequence of the holotype. Sample NVG-15026F10, GenBank PV550001, 658 base pairs:

AACTTTATATTTTATTTTCGGAATCTGAGCAGGAATAGTAGGTACTTCCCTAAGATTATTAATTCGAACTGAATTAGGAACTCCTGGATCATTAATTGGAGATGATCAAATTTACAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGTTTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCTGACATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGAGCTGGAACAGGATGAACAGTTTACCCCCCTTTATCTGCTAACATTGC
CCACCAAGGGTCTTCAGTAGATTTAGCTATTTTTTCCCTTCATTTAGCTGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACTGCACTACTTTTATTATTATCTTTACCTGTATTAGCAGGTGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCGGGAGGAGGAGATCCAATTCTTTACCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Figs. 47a and 51o (genitalia Fig. 36p–w), bears the following five printed (text in italics handwritten) rectangular labels, four white: [Rancho Grande. 1200 m. | Parque Nac. Henri Pittier | Edo. Aragua, Venezuela | T.E. Pliske *VI-29-75*], [Genit. Prep. | SRS-*1278*], [Allyn Museum | Acc. 19*80-29*], [DNA sample ID: | NVG-15026F10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | venezuelius Grishin]. **Paratypes:** 2♂♂ and 2♀♀ from Venezuela, Argua: 1♀ NVG-15026F11 the same data as the holotype, genitalia SRS-1279 (Figs. 47b, 51p) and 1♀ NVG-14062C01 Eancho Grande, 1100 m, 19-Jun-1985, S. S. Nicolay leg. [USNM]; 1♂ NVG-14113A05 Yuracay, Hacienda Tropicale ca.10 km S of San Felipe, 100–400 m, GPS 10.2917, −68.6667, 26-Jan-23-Feb-1993, Kareofelas & Witham leg. [LACM]; and 1♂ NVG-15032C11 (leg DNA extraction, sequenced), NVG-24028H11 (abdomen DNA extraction and dissection) Carabobo, Puerto Cabello, no date [around 1900], Hahnel leg., genitalia vial NVG241114-17 (Fig. 36x–z) [MFNB].

Type locality. Venezuela: Aragua, Henri Pittier National Park, Rancho Grande, elevation 1200 m.

Etymology. The name is given for the country with the type locality and to rhyme with its related species, *E. aequatorius*. The name is treated as an adjective.

Distribution. Venezuela.

Entheus ecuadius Grishin, new species

http://zoobank.org/297F3822-5303-4CE1-8706-08138124207A

(Figs. 34j–k, 44 part, 48, 50 part, 51q)

Definition and diagnosis. A female from Ecuador is sister to *Entheus dius* Mabille, 1898, **stat. rest.** (type locality in Brazil) and is genetically differentiated from it at the species level (Figs. 44, 50); e.g., their COI barcodes differ by 2% (13 bp), thus representing a new species. This new species keys to "*Entheus matho dius*" (B.10.5(d)) in Evans (1952) but differs from its relatives by a combination of the following characters: the white area on the hindwing widening towards the inner margin instead of being constricted towards it at vein 1A+2A, smaller white spots on the forewing, and larger separation between the discal cell spot and the spot in cell CuA_1-CuA_2. Due to the cryptic nature of this species and unexplored

Fig. 48. *Entheus ecuadius* **sp. n.** holotype ♀ NVG-14062C11 in dorsal (left) and ventral (right) views, data in text.

individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1651.31.1:G24A, aly1651.31.1:A95T, aly2548.15.2:T124C, aly2548.15.2:G168A, aly2548.15.2:C184T, aly1838.35.3:T48T (not C), aly1838.35.3:A66A (not G), aly1838.35.3:T112T (not A), aly6841.32.4:T1008T (not C), aly6841.32.4:T1014T (not A); and COI barcode: T97C, T157T (not C), A316G, T352C, T542T (not C), T595T (not C).

Barcode sequence of the holotype. Sample NVG-14062C11, GenBank PV550002, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGATTATTAATTCGAACTGAATTAGGAACCCCTGGATCATTAATCGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCAATTATAATTGGAGGTTTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGTTTTTGACTTCTACCCCCATCATTAACATTATTAATTTCTAGAAGAATTGTTGAAAATGGGGCTGGAACAGGATGAACAGTTTATCCTCCTTTATCCGCTAACATTGC
CCATCAAGGATCTTCAGTAGATTTAGCTATTTTTTCCCTTCATTTAGCTGGTATCTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATCTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACTGCATTACTTTTATTATTATCTTTACCTGTATTAGCAGGAGCTATTACTATACTTTTAACAGATCGAAATTTAAATACAT
CATTTTTTGACCCTGCTGGGGGGGGGGATCCAATTCTTTATCAACATTTATTT

Type material. Holotype: ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Figs. 48 and 51q (genitalia Fig. 34j–k), bears the following five printed (text in italics handwritten) rectangular labels, four white: [ECUADOR Napo | Archidona 800m | *10 Nov. '88* | S.S. Nicolay], [DNA sample ID: | NVG-14062C11 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E03 | c/o Nick V. Grishin], [genitalia: | NVG240817-42 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Entheus | ecuadius Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Type locality. Ecuador: Napo Province, Archidona, elevation 800 m.

Etymology. The name is formed from the name of its sister species by adding *ecua-* for the county with the type locality. The name is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in the eastern slopes of the Andes of central Ecuador.

Entheus bogoteus Grishin, new species

http://zoobank.org/CA6E6079-3FF2-4347-85D2-AC646FD0EB9F

(Figs. 44 part, 49, 50 part, 51r)

Definition and diagnosis. A male from Bogota, Colombia, identified as *Entheus latifascius* M. Hering, 1925, **stat. rest.** (type locality Colombia, Chocó, Rio Micay) is phylogenetically distant and not monophyletic with it, and instead is sister to *Entheus warreni* Grishin, 2012 (type locality in Ecuador: Esmeraldas), being genetically differentiated from it at the species level (Figs. 44, 50); e.g., their COI barcodes differ by 3.0% (20 bp), thus representing a new species. This new species keys to "*Entheus matho latifascius*" (B.10.5(b)) in Evans (1952), males of which he misidentified and incorrectly associated with females, and differs from its relatives by a combination of the following characters: forewing discal band is orange, partly hyaline towards its outer margin, where it is yellower, lacking an

Fig. 49. *Entheus bogoteus* **sp. n.** holotype ♂ NVG-22042E08 in dorsal (left) and ventral (right) views, data in text. The inset shows the hindtibial tuft enlarged two times compared to the specimen (scale not given).

orange streak between the costa and the discal cell reaching towards the wing base, but thicker towards the costa, and the two posterior semi-hyaline spots of the subapical band are strongly (by more than half of their width) offset distad from the rest; the anal fold is creamy-white, slightly yellower towards its sides; the hindtibial tuft is tawny. Due to unexplored individual variation in this species and the lack of known females, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly2012.50.2:C133A, aly2012.50.2:C153T, aly5719.4.12:C177G, aly144.43.21:C132A, aly144.43.21:C141G, aly304.5.1:A60A (not G), aly275211.5.10:T849T (not C), aly5294.1.1:T840T (not C), aly923.16.7:C468C (not T); and COI barcode: A61G, A91G, T284C, A312G, T376C, T427T.

Barcode sequence of the holotype. Sample NVG-22042E08, GenBank PV550003, 658 base pairs:

AACTTTATATTTTATTTTCGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGATTATTGATTCGAACTGAATTAGGAACTCCAGGATCGTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACTGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGGGGATTTGGAAATTGATTAGTACCTTTAATATTGGGAGCCCCTGATATAGCTTTTCCTCGGA
TAAATAATATAAGTTTTTGACTTCTACCCCCATCATTAACACTATTAATTTCTAGAAGAATTGTTGAAAGTGGAGCTGGAACAGGATGAACTGTTTATCCCCCTTTATCTGCTAATATTGC
CCATCAAGGATCCTCAGTAGATTTAGCTATTTTTTCCCTTCACTTAGCTGGTATTTCATCAATCTTAGGGGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACCGCATTACTTTTATTATTATCATTACCTGTATTAGCTGGTGCTATTACTATACTTTTAACAGATCGAAACTTAAATACAT
CATTTTTTGATCCTGCAGGAGGGGGAGATCCAATTCTCTATCAACATTTATTT

Type material. Holotype: ♂ deposited in the collection of the Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA (ANSP), illustrated in Figs. 49 and 51r, bears the following four printed (text in italics handwritten) rectangular labels, three white: [BOGOTA | COLOMBIA], [U. S. N. M. | *DIUS MAB.* | *?*], [DNA sample ID: | NVG-22042E08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Entheus | bogoteus Grishin].

Type locality. Colombia: Bogotá.

Etymology. The name is formed from the type locality and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in Bogotá, Colombia.

A preliminary taxonomic list of *Entheus* Hübner, [1819] species

Here, we integrate our new results into the previous taxonomic arrangement of *Entheus* Hübner, [1819] (Evans 1952; Steinhauser 1989; Austin 1997; Austin et al. 1997; Mielke 2005; Grishin 2013) to compile a preliminary taxonomic list for the genus and suggest a phylogenetic order of the species. The phylogeny of *Entheus* (Fig. 50) generally agrees with phenotypic considerations and division into species groups. The *eumelus*, *gentius*, *priassus*, and *matho* groups agree with the Evans's (1952) identification key. However, we find that *E. warreni* and *E. bogoteus* **sp. n.**, both of which would be identifiable as members of the *matho* group by the presence of a separate orange spot between the forewing orange bands in males, are not monophyletic with *E. matho* and form a clade sister to the *priassus* group. Therefore, we define a separate species group for them. Furthermore, in agreement with discussions by Austin (1997) and Austin et al. (1997) based on phenotypic differences and similarities, we partition the *priassus* group into three subgroups, distinguishing the *telemus* and *pralina* subgroups, which are closely related to each other and fully separate only in the nuclear genome tree (Fig. 50a).

We attempt to order species to maximize the phenotypic similarity and geographic proximity of the list neighbors but without disrupting phylogenetic orders given in genomic trees (Fig. 50): i.e., a strongly supported clade in the trees is a continuous segment in the list. The evolution and diversification of *Entheus* are riddled with complexities due to the incongruence of the genomic trees (Fig. 50). Most notably, *Entheus latifascius* M. Hering, 1925, **stat. rest.** (type locality in Colombia: Rio Micay) is confidently placed deep within the *matho* group in the nuclear genome tree inferred from autosomes (Fig. 50a), but is sister to the *priassus* group in both the Z chromosome and the mitochondrial genome trees (Fig. 50b, c). Until such discrepancies are explained, we side with phenotypic similarity in choosing between the conflicting phylogenetic hypotheses in different phylogenetic trees. Here, we chose to order species groups to maintain the traditional order of Evans (1952), which agrees with phylogenetic trees. Within each group, species are arranged to maximize wing pattern resemblance (within phylogenetic constraints) between neighboring species from different groups, i.e., the brightest member of the *priassus* group (e.g., *E. telemus*) is placed after the gentius group species consisting of brightly colored species,

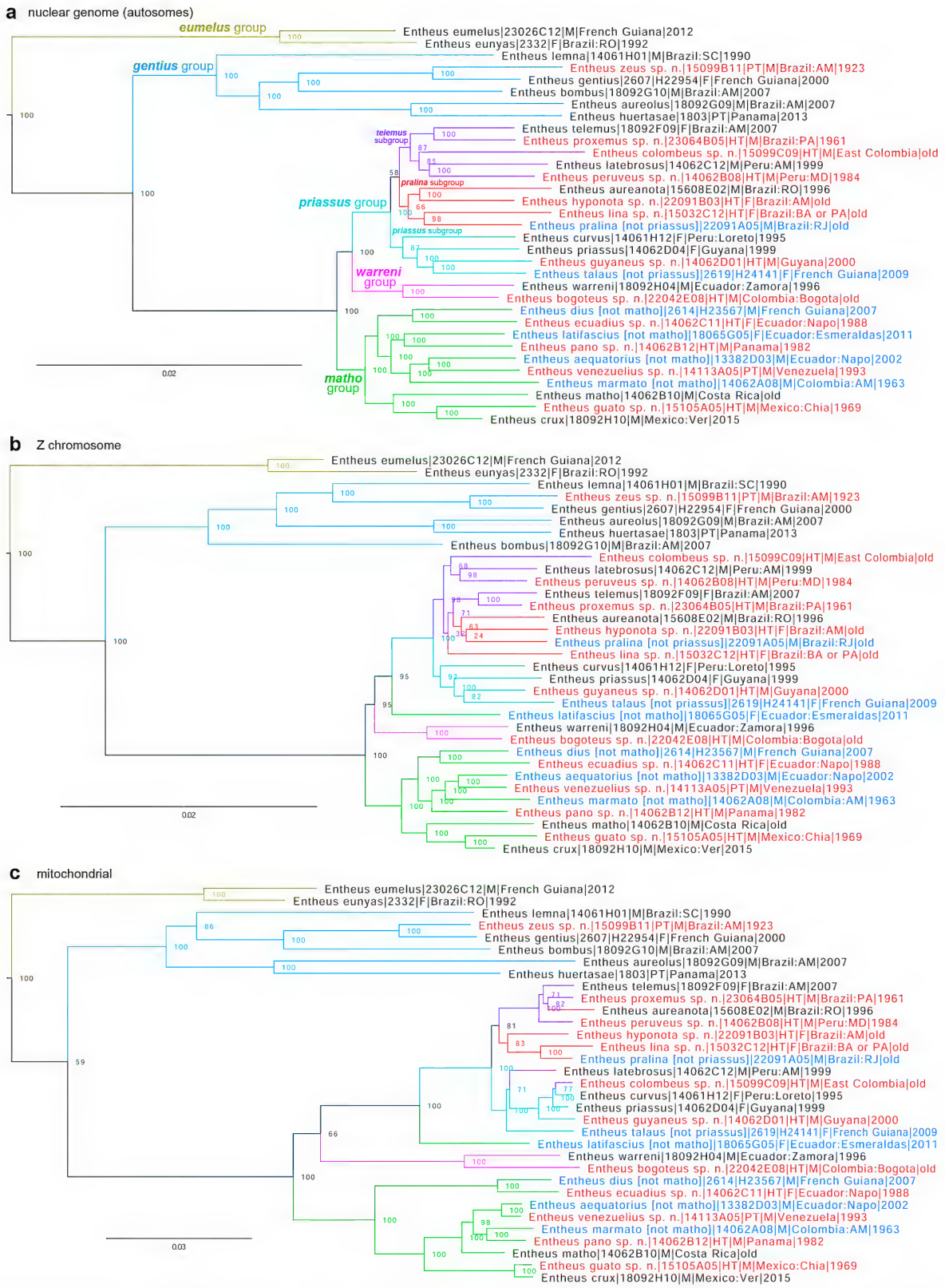


Fig. 50. Phylogenetic trees of *Entheus* inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 3,486,282 positions, **b)** the Z chromosome, based on 279,462 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species groups and subgroups are colored: *eumelus* group (olive), *gentius* group (blue), *priassus* group (cyan, with *telemus* and *pralina* subgroups in purple and red, respectively), *warreni* group (magenta), and *matho* group (green). New taxa proposed in this work are labeled in red, and those with taxonomic changes, such as subspecies-to-species or synonym-to-species status (changes indicated in brackets), are labeled in blue.

Fig. 51. *Entheus* specimens already illustrated above (data in text) shown life-size if printed on 8.5 by 11-inch paper for size comparison in dorsal (above each panel letter) and ventral (below) views: **a)** *E. zeus* **sp. n.** HT; **b, c)** *E. priassus*: **b)** NT, **c)** NT of =*P. peleus*; **d)** *E. talaus* **stat. rest.** NT & LT of =*Ph. serenus*; **e, f)** *E. guyaneus* **sp. n.**: **e)** HT, **f)** PT; **g)** *E. lina* **sp. n.** HT; **h)** *E. colombeus* **sp. n.** HT; **i)** *E. proxemus* **sp. n.** HT; **j, k)** *E. peruveus* **sp. n.**: **j)** PT, **k)** HT; **l)** *E. hyponota* **sp. n.** HT; **m)** *E. guato* **sp. n.** HT; **n)** *E. pano* **sp. n.** HT; **o, p)** *E. venezuelius* **sp. n.**: **o)** HT, **p)** PT; **q)** *E. ecuadius* **sp. n.** HT; **r)** *E. bogoteus* **sp. n.** HT.

and *E. dius* with the dark anal fold similar to the *priassus* group is near the beginning of the *matho* group. This arrangement results in the placement of *E. crux* and *E. guato* **sp. n.**, large species with dark females without a white area on the hindwing, last. Further refinements of the list order are encouraged.

In the resulting arrangement below, we also include two species discovered by Burns and co-authors (Janzen et al. 2011) but still unnamed, shown in gray font. Based on COI barcode comparison, we hypothesize that the third species, *Entheus* Burns03, may be conspecific with *E. matho*. Type localities (general area only: state, region, department, or county) are in gray font. New taxa described in this study and the category of taxonomic change are in red font. Taxonomic treatment before this work (for valid names) or the category of synonym (for synonyms) and comments (phenotypic characters for species groups and subgroups refer to males) are shown in smaller font following a vertical bar | after the type locality; an equal sign = precedes synonyms given in their original genus combination; and a double dagger ‡ marks permanently invalid synonyms (e.g., objective synonyms) and unavailable names. The list covers 36 valid taxa, all at the species level, with 12 newly proposed here (and 2 yet undescribed) and 6 elevated (from subspecies or synonyms) to the species status: i.e., 16 previously listed as species with 5 additional subspecies and 1 synonym: 22 known and 14 undescribed before this work. Our study follows the trend to reveal approximately as many new Hesperiidae taxa as previously described ones in nearly every genus under revision (Austin and Mielke 1998; Austin and Mielke 2008; Medeiros et al. 2019; Siewert et al. 2020). Because our work on *Entheus* has not been completed yet, the list below is preliminary, given as a guide to the published knowledge, and with additions to follow.

Genus ***Entheus*** Hübner, [1819]; type species *Papilio peleus* Linnaeus, 1763

eumelus species group | no tibial tuft

Entheus eumelus (Cramer, 1777): Suriname

= *Entheus mina* Williams & Bell, 1931; Suriname | junior subjective synonym

Entheus eunyas Austin, O. Mielke & Steinhauser, 1997: Brazil: Rondônia

Entheus ninyas H. Druce, 1912; Bolivia: La Paz

gentius species group | wing bases yellow, orange, or tawny above, tibial tuft present

Entheus lemna (A. Butler, 1870): not given [Brazil: Minas Gerais from later work (Butler 1872)]

= *Phareas berytus* Hewitson, 1877; not given [Brazil: Espirito Santo on label] | junior subjective synonym

= *Phareas annae* Plötz, 1883; Brazil: Pará | junior subjective synonym

= *Entheus schmithi* F. Hoffmann, 1932; Brazil: Santa Catarina | junior subjective synonym

Entheus zeus Grishin, **sp. n.**: Brazil: Amazonian region

Entheus gentius (Cramer, 1777): Suriname

= *Entheus concinna* Plötz, 1883; Brazil: Pará | junior subjective synonym

=‡ *Entheus osiris* Plötz, 1883; Brazil: Pará | nomen nudum (proposed in synonymy)

= *Entheus sirius* Mabille, 1898; "Cayenne" [? French Guiana] | junior subjective synonym

Entheus bombus Austin, O. Mielke & Steinhauser, 1997: Brazil: Rondônia

Entheus aureolus Austin, O. Mielke & Steinhauser, 1997: Brazil: Rondônia

Entheus huertasae Grishin, 2013; Colombia

priassus species group | forewing spot attached to the discal band, tibial tuft present

telemus species subgroup | tibial tuft brown, tibial brush brown to orange

Entheus telemus Mabille, 1898; Brazil [Amazonas]

Entheus proxemus Grishin, **sp. n.**: Brazil: Pará

Entheus colombeus Grishin, **sp. n.**: E Colombia

Entheus latebrosus Austin, 1997; Ecuador: Limoncocha

Entheus peruveus Grishin, **sp. n.**: Peru: Madre de Dios

pralina species subgroup | tibial tuft brown, tibial brush brown to orange

Entheus aureanota Austin, O. Mielke & Steinhauser, 1997: Brazil: Rondônia

Entheus hyponota Grishin, **sp. n.**: Brazil: Amazonas

Entheus lina Grishin, **sp. n.**: Brazil: Pará

Entheus pralina Evans, 1952, **stat. nov.**; Brazil: Espirito Santo | was a subspecies of *priassus*

priassus species subgroup | tibial tuft and brush yellow

Entheus curvus Austin, 1997; Peru: Loreto

Entheus priassus (Linnaeus, 1758); Suriname

= *Papilio peleus* Linnaeus, 1763; French Guiana | junior subjective synonym

= *Entheus cramerianus* Mabille, 1898; S. America | junior subjective synonym

Entheus guyaneus Grishin, **sp. n.**; Guyana

Entheus talaus (Linnaeus, 1763), **stat. rest.**; S. America [? Brazil: Pará] | was a synonym of *priassus*

= *Peleus aeacus* Swainson, 1831; French Guiana | junior subjective synonym

=‡ *Phareas serenus* Plötz, 1883; S. America [? Brazil: Pará] | junior objective synonym

warreni species group | forewing spot detached from the discal band, submarginal doublet offset, tibial tuft tawny

Entheus warreni Grishin, 2012; Ecuador: Esmeraldas

Entheus bogoteus Grishin, **sp. n.**; Colombia: Bogota

matho species group | forewing spot detached from the discal band, tibial tuft tawny to yellow

Entheus latifascius M. Hering, 1925, **stat. rest.**; Colombia: Chocó, Rio Micay | was a subspecies of *matho*

= *Entheus quadratus* Bargmann, 1929; W Colombia: Rio Dagua | junior subjective synonym

Entheus dius Mabille, 1898, **stat. rest.**; Brazil [Amazonian region] | was a subspecies of *matho*

Entheus ecuadius Grishin, **sp. n.**; Ecuador: Napo

Entheus aequatorius Mabille & Boullet, 1919, **stat. rest.**; "Bolivia" [Ecuador] | was a ssp. of *matho*

Entheus venezuelius Grishin, **sp. n.**; Venezuela: Aragua

Entheus marmato Salazar & Vargas, [2017], **stat. nov.**; Colombia: Caldas | was a subspecies of *matho*

Entheus pano Grishin, **sp. n.**; Panama: Darién

Entheus sp. undescribed Burns01; Costa Rica

Entheus matho Godman & Salvin, 1879; Nicaragua | likely conspecific with *Entheus* Burns03

Entheus sp. undescribed Burns02; Costa Rica

Entheus guato Grishin, **sp. n.**; Mexico: Chiapas

Entheus crux Steinhauser, 1989; Mexico: Veracruz

Tribe Eudamini Mabille, 1877

The holotype of *Cecropterus* (*Thorybes*) *oaxacensis* Grishin, 2023

The original description illustrated the holotype of *Cecropterus* (*Thorybes*) *oaxacensis* Grishin, 2023 (type locality Mexico: Oaxaca, Tlalixtac de Cabrera, Hwy 175, ca. 5 mi north of Oaxaca City) when it

Fig. 52. Holotype of *Cecropterus* (*Thorybes*) *oaxacensis* ♂ NVG-19125B09 in dorsal (left) and ventral (right) views.

was pinned through its side, unspread (Zhang et al. 2023b). Here, we use this opportunity and publish photographs of the holotype after it has been dissected and spread, to facilitate recognition of this specimen (Fig. 52). The holotype is in the University of Texas Insect Collection, Austin, TX, USA.

Cecropterus (*Thorybes*) *coxeyi* (Williams, 1931) is a species distinct from *Cecropterus* (*Thorybes*) *egregius* (Butler, 1870)

Genomic analysis of *Eudamus coxeyi* Williams, 1931 (type locality Ecuador: Huigra, holotype sequenced as NVG-15096B02), currently treated as a subspecies of *Cecropterus* (*Thorybes*) *egregius* Butler, 1870 (type locality not specified), reveals that the two taxa are genetically differentiated at the species level (Fig. 53); e.g., their F_{st}/G_{min}/COI barcode difference are 0.37/0.014/1.2% (8 bp). The former taxon differs from the latter by being paler: e.g., forewing semi-hyaline spots are larger, the ventral hindwing ground color is pale brown, and hindwing fringes are white (Evans 1952). Therefore, we propose that *Cecropterus* (*Thorybes*) *coxeyi* (Williams, 1931), **stat. rest.** is a species distinct from *Cecropterus* (*Thorybes*) *egregius* (Butler, 1870). As a result, *C. egregius* becomes monotypic. The COI barcode sequence of the holotype of *C. coxeyi*, sample NVG-15096B02, GenBank PV550004, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCATTAAGTTTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATCGGAGGATTTGGAAATTGATTAGTTCCTCTTATATTAGGAGCTCCTGATATAGCTTTCCCTCGTA
TAAATAATATAAGATTTTGATTATTACCCCCTTCATTAACTCTTTTAATTTCAAGAAGTATTGTTGAAAATGGTGCAGGTACTGGTTGAACTGTTTACCCCCCTTTATCTTCTAATATTGC
TCATCAAGGAGCATCAGTAGATTTAGCAATTTTTTCTTTACATCTTGCAGGAATTTCATCTATTCTTGGAGCTATTAATTTTATCACAACTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCATTATTTATTTGAGCTGTTGGAATTACAGCTCTACTTTTATTACTTTCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGAAACTTAAATACTT
CATTTTTTGATCCTGCAGGTGGGGGAGATCCTATTTTATATCAACATTTATTT

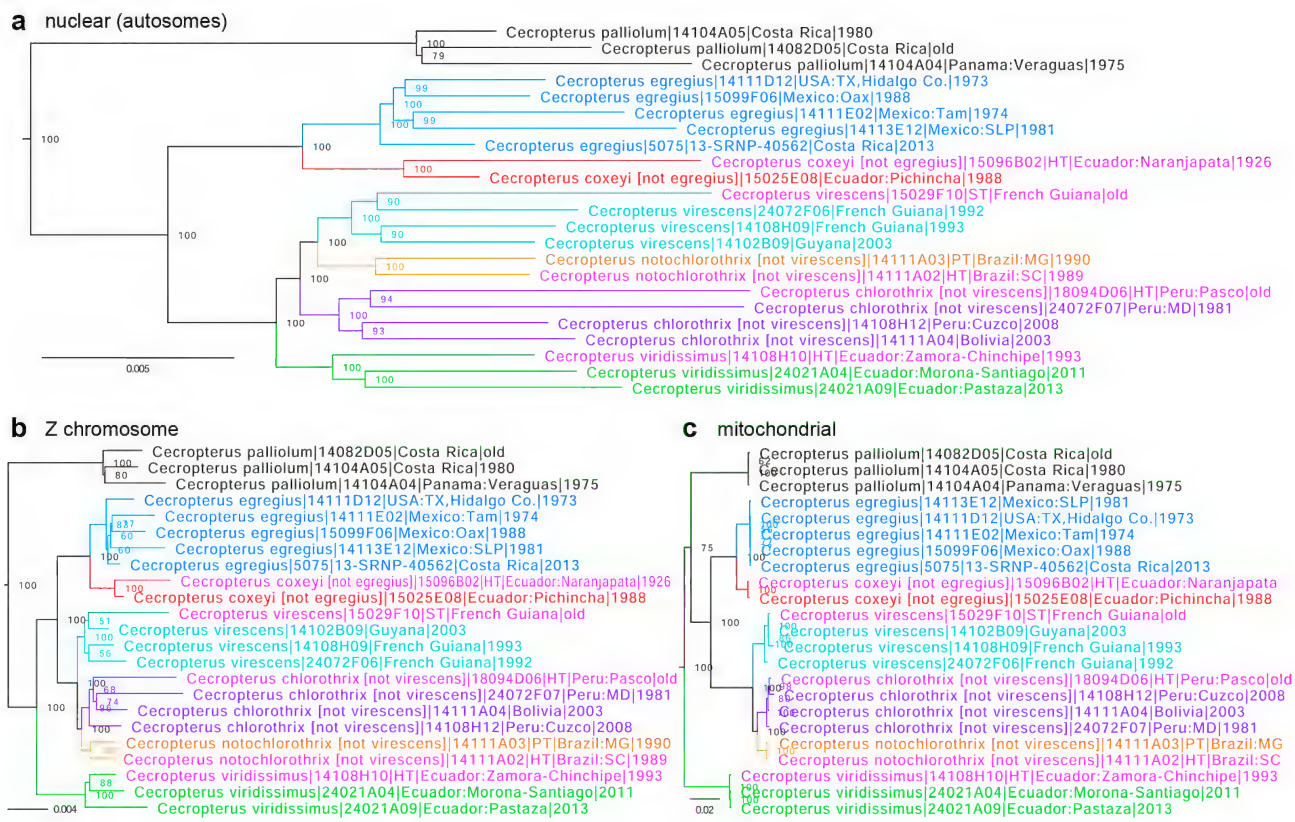


Fig. 53. Phylogenetic trees of selected *Cecropterus* (*Thorybes*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 11,630,790 positions, **b)** the Z chromosome, based on 338,631 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species are colored differently: *C. egregius* (blue), *C. coxeyi* **stat. rest.** (red), *C. virescens* (cyan), *C. chlorothrix* (purple), *C. notochlorothrix* **sp. n.** (orange), and *C. viridissimus* (green). Primary type specimens are labeled in magenta.

Cecropterus (*Thorybes*) *chlorothrix* (Röber, 1925) is a species distinct from *Cecropterus* (*Thorybes*) *virescens* (Mabille, 1877)

Genomic analysis of *Eudamus chlorothrix* Röber, 1925 (type locality Peru: Pasco, Huancabamba, holotype sequenced as NVG-18094D06), currently treated as a junior subjective synonym of *Cecropterus* (*Thorybes*) *virescens* (Mabille, 1877) (type locality given as "Cayenne" [French Guiana?], syntype sequenced as NVG-15029F10), reveals that the two taxa are genetically differentiated at the species level (Fig. 53); e.g., their F_{st}/G_{min}/COI barcode difference are 0.18/0.012/2.3% (15 bp). Therefore, we propose that *Cecropterus* (*Thorybes*) *chlorothrix* (Röber, 1925), **stat. rest.** is a species distinct from *Cecropterus* (*Thorybes*) *virescens* (Mabille, 1877). The COI barcode sequence of the holotype of *C. chlorothrix*, sample NVG-18094D06, GenBank PV550005, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCATTAAGTTTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCCCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAATTCCTCTTATATTAGGAGCTCCTGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCTCCCTCTTTAACTCTTTTAATTTCAAGAAGTATTGTTGAAAATGGTGCGGGTACTGGTTGAACTGTTTATCCCCCTTTATCTTCTAATATTGC
CCATCAAGGAGCATCAGTAGATTTAGCAATTTTTTCATTACATCTTGCAGGAATTTCATCTATTCTTGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCATTATTTATTTGAGCTGTTGGAATTACAGCTTTATTATTATTACTTTCACTACCTGTTTTAGCTGGGGCCATTACTATACTATTAACTGATCGAAACTTAAATACTT
CATTTTTTGATCCTGCAGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Cecropterus (*Thorybes*) *notochlorothrix* Grishin, new species

http://zoobank.org/F47CF66E-9C31-4CBB-8789-B5F42D7DEC04

(Figs. 53 part, 54, 55a–b)

Definition and diagnosis. In addition to *Cecropterus* (*Thorybes*) *virescens* (Mabille, 1877) (type locality given as "Cayenne" [French Guiana?]) and *Cecropterus* (*Thorybes*) *chlorothrix* (Röber, 1925), **stat. rest.** (type locality Peru: Pasco, Huancabamba), genomic analysis reveals a third clade in this group genetically differentiated from the others at the species level (Fig. 53). This clade is sister to *C. virescens* in the nuclear genome (autosomes) tree (Fig. 53a) but is sister to *C. chlorothrix* in the Z chromosome (Fig. 53b) and the mitochondrial genome trees (Fig. 53c). Its F_{st}/G_{min}/COI barcode difference are 0.23/0.005/2.0% (13 bp) (from *C. virescens*) and 0.17/0.012/1.4% (9 bp) (from *C. chlorothrix*). Therefore, this clade represents a new species. This new species keys to "*Urbanus virescens*" (C.13.27) in Evans (1952) but differs from its relatives by the following combination of characters: a distally rounded harpe (Fig. 55a) (more pointed in *C. chlorothrix*) without the distal and central broad projections of *C. virescens* (Fig. 55e, f) and with a narrower dorsal projection similar to that in *Cecropterus* (*Thorybes*) *viridissimus* Grishin, 2023 (type locality in Ecuador), which in addition possesses dull distal and central projections;

Fig. 54. *Cecropterus* (*Thorybes*) *notochlorothrix* **sp. n.** holotype ♂ NVG-14111A02 in dorsal (left) and ventral (right) views.

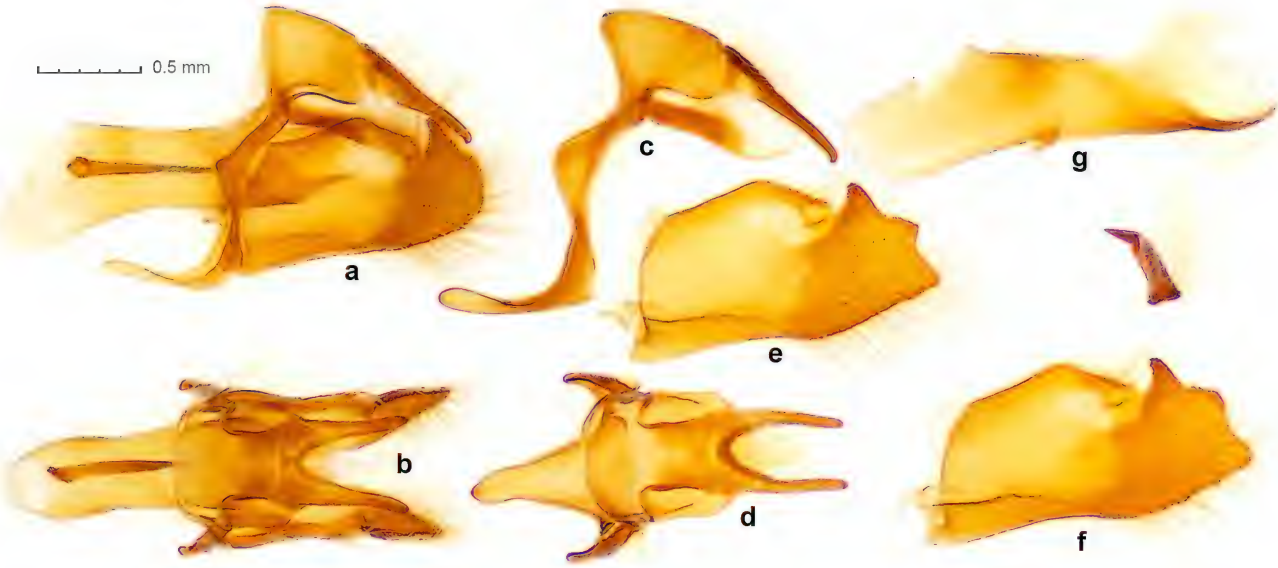


Fig. 55. Male genitalia of *Cecropterus* (*Thorybes*), data in text or below [MGCL]: **a–b)** *C.* (*T.*) *notochlorothrix* **sp. n.** paratype NVG-24124A07 Brazil, São Paulo, complete genital capsule and **c–g)** *C.* (*T.*) *virescens* NVG-24124A03 French Guiana, Saül, 8-Jun-1992, L. Sénécaux & A. Docquin leg., vial SRS-5288: **c–d)** genitalia with **e)** left and **f)** right valvae and **g)** aedeagus (vesica everted, cornutus below) detached and shown separately: in **a, c, e–g)** left lateral and **b, d)** dorsal views.

slightly thicker and shorter uncus arms (Fig. 55a vs. c) that are more strongly diverging (Fig. 55b vs. d); a straighter dorsal surface of the tegumen and a more angled anteriad (vs. rounder) central bend in the vinculum in lateral view (Fig. 55a vs. c); a narrower forewing and a more elongated towards the tornus hindwing; generally darker facies, narrower semi-hyaline white spots and bars on the forewing, especially the subapical spots, and typically stronger overscaled with brown (within the white marginal band) apex of the ventral hindwing. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly11426.2.3:C135G, aly11426.2.3:G141A, aly11426.2.3:C153A, aly18826.19.9:G42A, aly18826.19.9:C75T; and COI barcode: T82C, A109G, A217G, T274C, 400A, 517C.

Barcode sequence of the holotype. Sample NVG-14111A02, GenBank PV550006, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCATTAAGTTTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAGATTTATAATACT
ATTGTTACAGCCCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAATTCCTCTTATATTAGGGGCTCCTGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCCCCCTCCTTAACTCTTTTAATTTCAAGAAGTATTGTTGAAAATGGTGCAGGTACTGGTTGAACTGTTTATCCCCCTTTATCTTCTAATATTGC
CCATCAAGGAGCATCAGTAGATTTAGCAATTTTTTCATTACATCTTGCAGGAATTTCATCTATTCTTGGAGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCATTATTTATTTGAGCTGTCGGAATTACAGCTTTATTATTATTACTTTCACTACCTGTTTTAGCTGGAGCCATTACTATATTATTAACTGATCGAAACTTAAATACTT
CATTTTTTGATCCTGCAGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 54, bears the following three printed (text in italics handwritten) rectangular labels, two white: [BRAZIL:Sta Catarina | Joinville, 0–200m | 26°19'S 48°53'W | *28.X.1989* | leg. H. Miers], [DNA sample ID: | NVG-14111A02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Cecropterus (Thorybes) | notochlorothrix Grishin]. **Paratypes:** 4♂♂ from Brazil: 1♂ NVG-14111A03 Minas Gerais, Viçosa, 650 m, approx. GPS −20.750, −42.867, 9.II.1990, H. Miers leg. [USNM] and São Paulo, São Paulo, D. L. Lindsley leg. [MGCL]: 1♂ NVG-24124A07 13-Aug-1960, genitalia NVG250517-04 (Fig. 55a–b) and 2♂♂ 26-Feb-1961: NVG-24124A08 and NVG-24124A09.

Type locality. Brazil: Santa Catarina, Joinville, elevation 0–200m, approx. GPS −26.3167, −48.8833.

Etymology. In Greek, νότιος (notios) means southern. This modified prefix is added to the name of a relative of the new species, *C. chlorothrix*, which itself is a composite of two Greek words: χλωρός (chloros) for green and θρίξ (trix) for hair, literally meaning green-haired. The name is treated as a noun in apposition.

Distribution. Currently known from Southeast and South Brazil.

Additional specimens of *Cecropterus* (*Thorybes*) *viridissimus* Grishin, 2023 confirm it as a species-level taxon

Cecropterus (*Thorybes*) *viridissimus* Grishin, 2023 (type locality in Ecuador) is an unusual species that is very similar in facies to *Cecropterus* (*Thorybes*) *virescens* (Mabille, 1877) (type locality given as "Cayenne" [French Guiana?]) and closely related to it in the protein-coding genes from autosomes (Fig. 53a), but is sister to both *C. virescens* and *Cecropterus* (*Thorybes*) *egregius* (A. Butler, 1870) (type locality unknown) in the Z chromosome and mitochondrial genome trees (Fig. 53b, c). Known only from its holotype, *C. viridissimus* might have been a hybrid or had contaminated DNA, thus explaining the phylogenetic incongruence. During further genomic sequencing, we stumbled upon two additional specimens of *C. viridissimus* (Figs. 53, 56), both from eastern Ecuador but from different localities distant from the type locality in the Andes of southern Ecuador. One of them is the first confirmed female of *C. viridissimus* (Fig. 56b). These specimens closely cluster with the holotype and display the same incongruence of the genomic trees, thus confirming *C. viridissimus* as a species (Fig. 53).

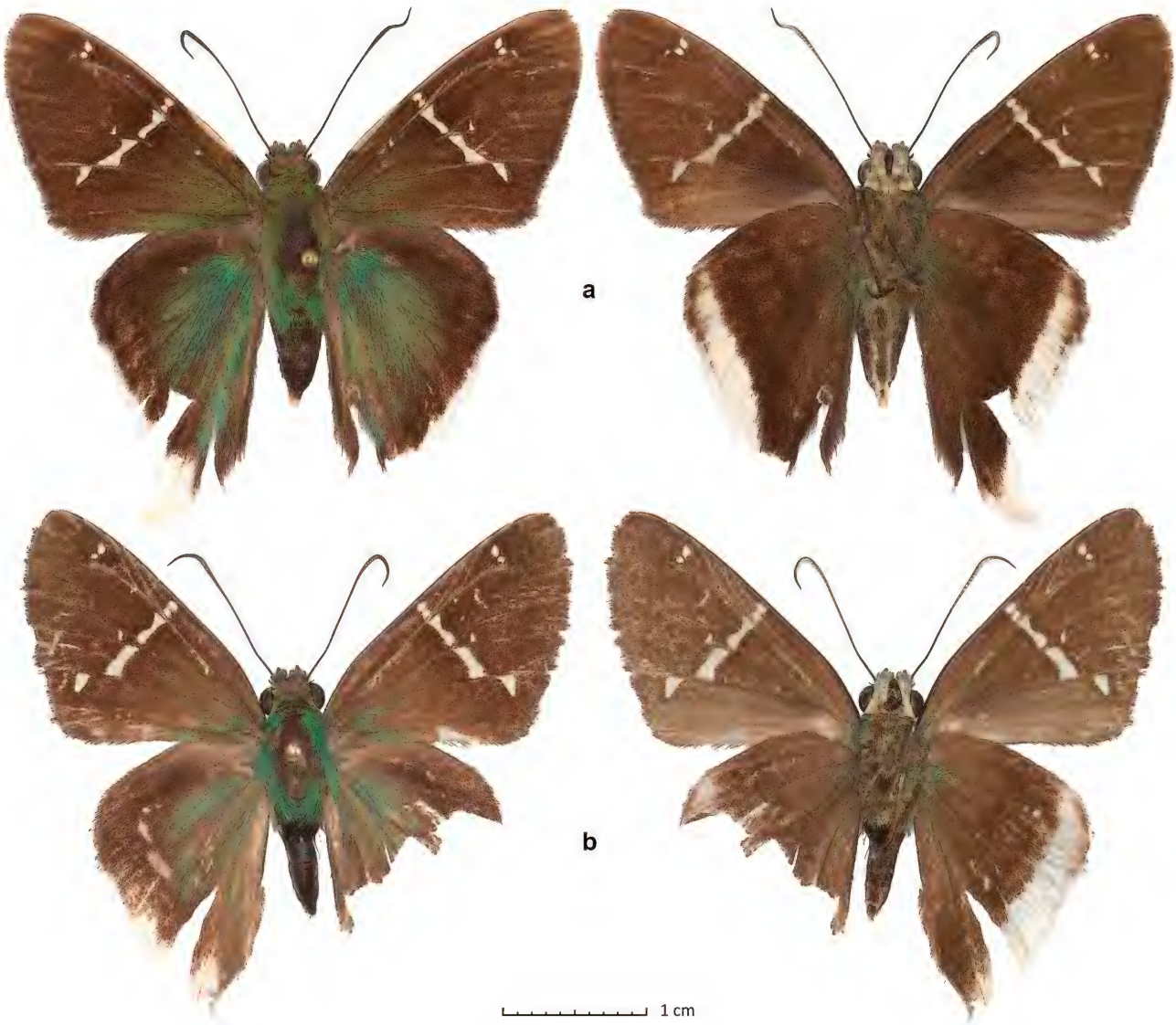


Fig. 56. A pair of *Cecropterus* (*Thorybes*) *viridissimus* from Ecuador [SMF] in dorsal (left) and ventral (right) views: **a)** ♂ NVG-24021A04 Morona-Santiago, San Isidro, Macas, 1250 m, −2.12, −78.10, 17-Dec-2011, J.-C. Petit leg. and **b)** ♀ NVG-24021A09 Pastaza, Puyo, Mirador Condor, 1200 m, −1.28, −77.48, 7-Nov-2013 J.-C. Petit, E. & J. Brockmann leg.

Aethilla toxeus Plötz, 1882 is confirmed as a junior subjective synonym of *Cecropterus* (*Murgaria*) *albociliatus albociliatus* (Mabille, 1877)

To put our surprising hypothesis that *Aethilla toxeus* Plötz, 1882 (type locality in Mexico) is a junior subjective synonym of *Cecropterus* (*Murgaria*) *albociliatus albociliatus* (Mabille, 1877) (type locality in Colombia, Panama, and Guatemala) (Zhang et al. 2023d) to further test and to determine the phylogenetic position of the lectotype more precisely, we sampled and sequenced another leg of the *A. toxeus* lectotype in MFNB along with additional specimens of *C. albociliatus*. Genomic phylogenetic trees place the new sample of *A. toxeus* (NVG-24028H08) together with the previously sequenced (NVG-15032A10) (Fig. 57

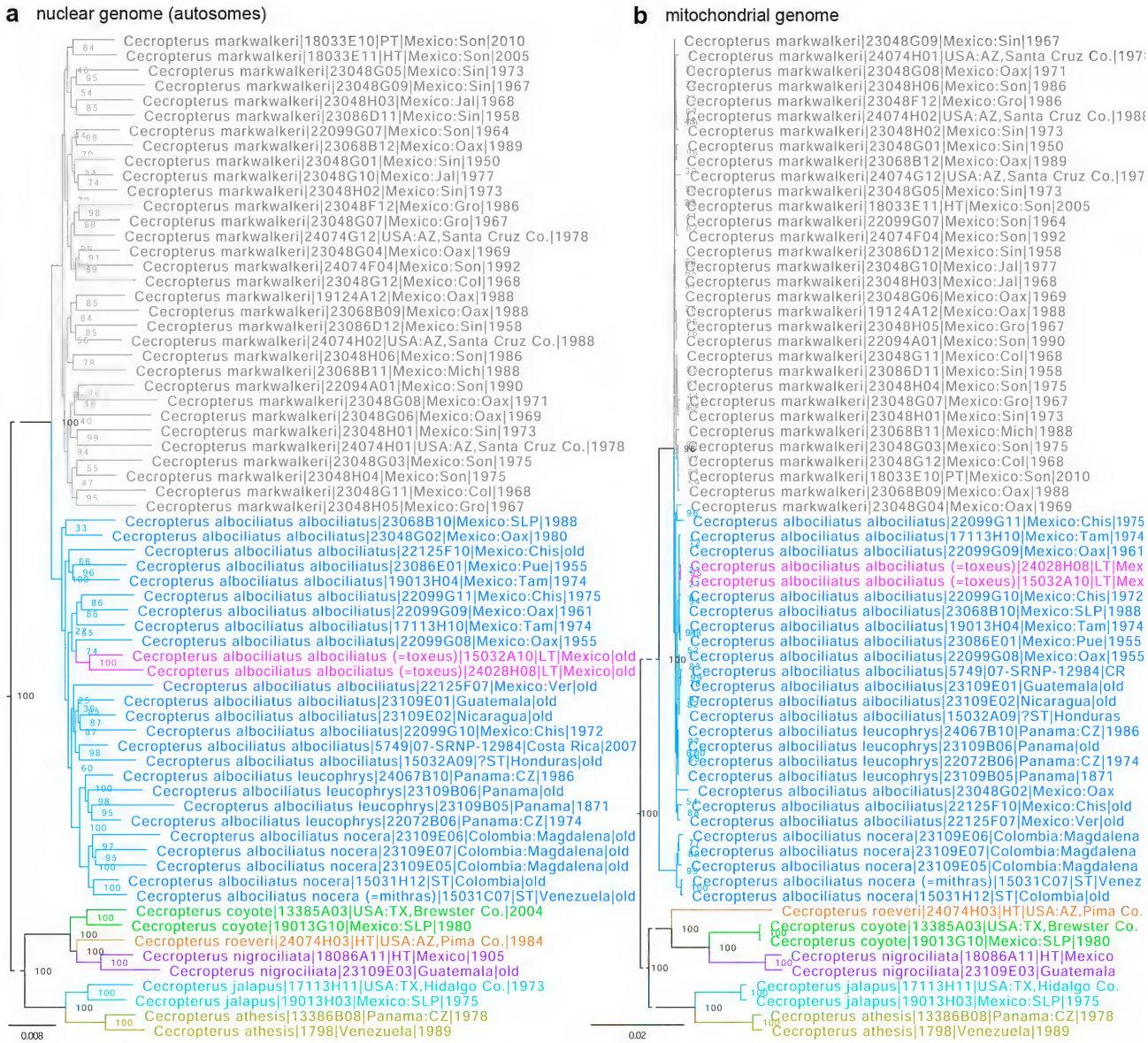


Fig. 57. Phylogenetic trees of selected *Cecropterus* (*Murgaria*) species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,538,820 positions, and **b)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species are colored differently: *C. markwalkeri* Grishin, 2023 (gray), *C. albociliatus* (blue, with the lectotype of *A. toxeus* in magenta), *C. coyote* (Skinner, 1892) (green), *C. roeveri* Grishin, 2025 (orange), *C. nigrociliata* (Mabille & Boullet, 1912) (purple), *C. jalapus* (Plötz, 1881) (cyan), and *C. athesis* (Hewitson, 1867) (olive). Gaps in branches indicate where vertical slices of the tree were removed to reduce its horizontal dimension (to allow an increase in the font size), i.e., branches with gaps are longer than shown.

magenta), thus confirming the synonymy. The COI barcode sequence of the lectotype, sample NVG-15032A10, GenBank PV550007, 658 base pairs, is:

AACCTTATATTTTATTTTTGGAATTTGAGCAGGATTAGTAGGAACTTCTTTAAGTTTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCTATTATAATTGGAGGATTTGGAAATTGACTAGTTCCCCTTATATTAGGAGCCCCTGACATAGCTTTCCCTCGTA
TAAATAATATAAGATTTTGATTATTACCCCCATCTTTAACTCTTTTAATTTCAAGAAGAATTGTAGAAAATGGTGCAGGTACTGGATGAACAGTTTATCCCCCTTTATCCTCTAATATTGC
CCACCAAGGAGCATCAGTAGATTTAGCAATTTTTTCTTTACATTTAGCTGGAATTTCTTCTATTCTTGGAGCTATTAACTTTATTACAACTATTATTAATATACGAATTAATAATTTATCA
TTTGATCAAATACCATTATTTATTTGAGCTGTCGGAATTACAGCCTTATTATTATTACTTTCTTTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCCGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Furthermore, in our previously published nuclear tree that was based on a small number of specimens (Zhang et al. 2023d), the lectotype of *A. toxeus* was sister to all other included specimens of *C. albociliatus* (even of other subspecies), albeit with a non-significant bootstrap support of 15% (fig. 8a in Zhang et al. 2023d). However, with additional specimens sequenced and the quality of the *A. toxeus* lectotype dataset improved by the second sequencing, it is now positioned within *C. albociliatus albociliatus* specimens (Fig. 57 magenta within blue), sister to one specimen from Mexico: Oaxaca with 74% bootstrap support in the nuclear genome tree (Fig. 57a). Although not sufficient for a confident conclusion, mainly because other specimens from Oaxaca are scattered throughout the phylogenetic tree, this position of the *A. toxeus* lectotype suggests that it might have been collected in Oaxaca. The collector of the lectotype, Ferdinand Deppe, indeed collected in Oaxaca, among several other places in southern Mexico (e.g., Veracruz) (Stresemann 1954). Moreover, the holotype of *Apyrrothrix araxes cyrillus* (Plötz, 1879), also collected by Deppe, is from Oaxaca. Additional genomic sequencing, coupled with population-level analysis of these datasets, may provide a more definitive answer regarding the provenance of the *A. toxeus* lectotype.

Urbanus (*Urbanoides*) *elma* Grishin, new species

http://zoobank.org/D77594CE-FE05-4EF4-94B2-5B45443632F7

(Figs. 58 part, 59)

Definition and diagnosis. A close sister to *Urbanus elmina* Evans, 1952 (type locality in Ecuador: Rio Pastaza), this new species keys to it (C.13.9) in Evans (1952) and Steinhauser (1981) and was included by them in that taxon, but is genetically differentiated from it at the species level (Fig. 58); e.g., their COI barcodes differ by 3.2% (21 bp). The new species shares with *U. elmina* its "washed out appearance" of ventral hindwing markings (Steinhauser 1981), i.e., darker bands are not prominent and are poorly contrasting with the ground color, but differs from *U. elmina* by a narrower and more elongated toward the tail hindwing and in females a narrower hindwing tail, wider semi-hyaline spots (e.g., in the forewing cell CuA_1-CuA_2), a more extended semi-hyaline spot reaching (and in females crossing) the middle of the forewing cell CuA_2-1A+2A, and slightly bluer (rather than greener) overscaling on the dorsal hindwing of females. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly27.17.6:C102G, aly3446.3.6:A40C, aly814.24.5:C36T, aly707.13.2:A96G, aly2178.51.8:A106G; and COI barcode: T43C, C220T, A268G, T439C, T581C, A619G.

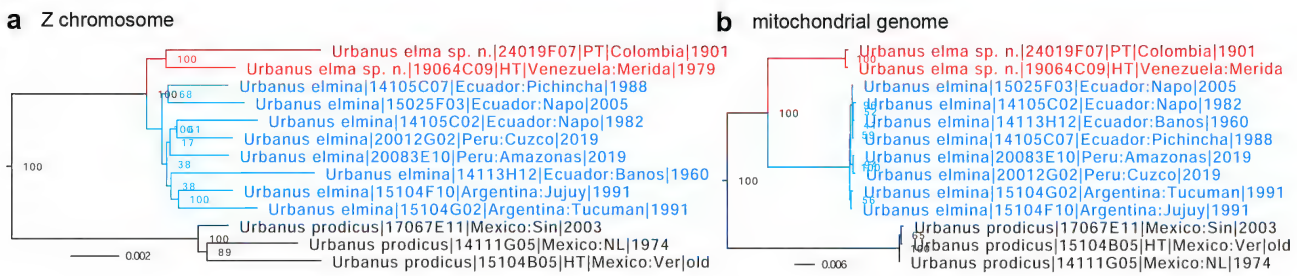


Fig. 58. Phylogenetic trees of selected *Urbanus* (*Urbanoides*) species (*U. elma* **sp. n.** in red and *U. elmina* in blue) constructed from protein-coding regions in: **a)** the Z chromosome, based on 615,213 positions, and **b)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

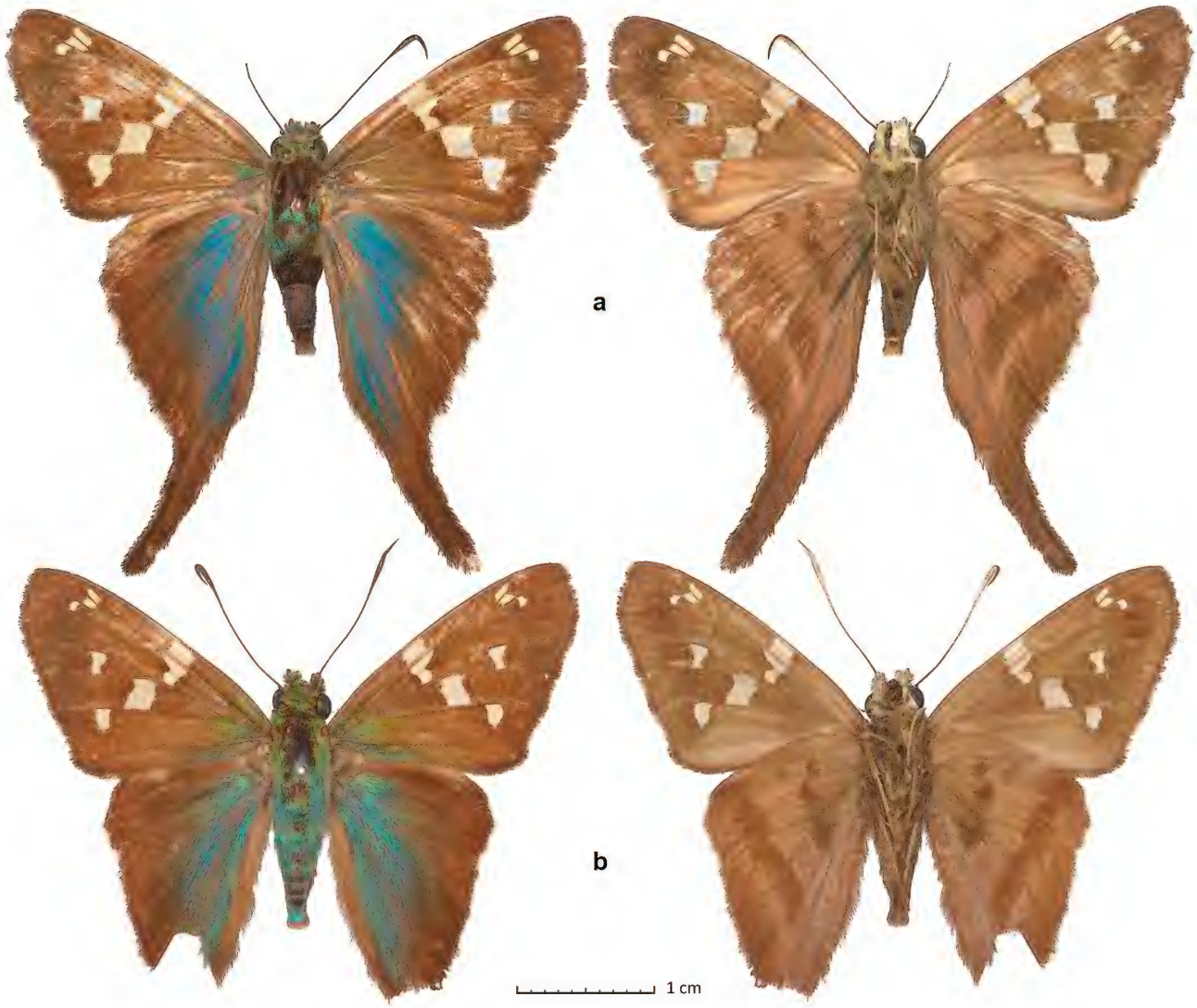


Fig. 59. *Urbanus* (*Urbanoides*) *elma* **sp. n.** in dorsal (left) and ventral (right) views, data in text:
a) holotype ♀ NVG-19064C09 from Venezuela and **b)** paratype ♂ NVG-24019F07 from Colombia.

Barcode sequence of the holotype. Sample NVG-19064C09, GenBank PV550008, 658 base pairs:

AACCTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGCACTTCATTAAGATTACTTATTCGAACTGAATTAGGAACCCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAATCCCCTTAATAATAGGAGCTCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGATTATTGCCACCTTCACTAACTTTATTAATCTCAAGAAGAATTGTTGAAAATGGTGCCGGTACTGGATGAACAGTTTATCCCCCCCTTTCATCTAATATTGC
CCATCAAGGAGCTTCTGTTGATTTAGCAATTTTTTCTCTACATCTTGCAGGTATTTCATCTATTCTTGGAGCTATCAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTACTATTATCTTTACCTGTTTTAGCAGGAGCTATTACTATATTACTAACTGATCGAAATTTAAATACCT
CCTTTTTTGATCCGGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the Bohart Museum of Entomology, University of California, Davis, CA, USA (UCDC), illustrated in Fig. 59a, bears the following five printed rectangular labels, four white: [Merida | Libertador | Merida VZLA | VII 3 1979], [J McLaughlin | A A Grigarick | R O Schuster | R W Brooks], [Urbanus elmina Evans, 1952 | female | Det. A. D. Warren, 2000], [DNA sample ID: | NVG-19064C09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Urbanus (Urbanoides) elma Grishin]. **Paratype:** 1♂ NVG-24019F07 Colombia (no details), 1901, Stichel [SMF] (Fig. 59b).

Type locality. Venezuela: Merida, Libertador, Merida.

Etymology. The name is formed from the name of its sister species, *U. elmina*, made shorter to indicate the more northern distribution of the new species. The name is a noun in apposition.

Distribution. Currently known from Colombia and Venezuela.

Lectotype designation for *Eudamus hopfferi* Plötz, 1881

Eudamus hopfferi Plötz, 1881 was described from an unstated number of specimens that also included specimen(s) considered by Herrich-Schäffer (1869) to be a variation of *Eudamus alector* C. Felder & R. Felder, 1867 (type locality Colombia: Bogota) (now *Telegonus alector alector*, see below) with the white forewing band reduced to a smear, and the locality for these specimens was given as "Süd-America" (South America) (Plötz 1881). The type specimens of *E. hopfferi* labeled as such are unknown. Our search in the MFNB collection for Herrich-Schäffer specimens (Herrich-Schäffer Hesperiidae are mostly in MFNB) matching the description was unsuccessful. However, inspecting an unpublished manuscript by Plötz in ZSMC dated 1876, which is an earlier version of his published Hesperiidae keys, we found additional information about *E. hopfferi* (Fig. 60c): "Mus. Berol. 4969", which is a reference to a specimen lot in MFNB with the number 4969. Plötz identified one (or more) specimen(s) in this lot as *E. hopfferi*, and therefore, such specimens (when agreeing with the original description) should be considered syntypes. While for many species described by Plötz, these specimen numbers were also listed in the published version of the keys, for *E. hopfferi*, the MFNB number was not given.

The catalog of historical MFNB collections handwritten by the Entomology curator Carl Heinrich Hopffer (died in 1876, before the description of *E. hopfferi*) contained an entry for the lot 4969 (Fig. 60d) showing that it was a single specimen collected by Deppe in Mexico and giving the name for it as "Hesperia phanaeus N." Ferdinand Deppe collected in Mexico in 1824–1829 (Stresemann 1954), and this specimen should have been collected then. The name "phanaeus" was not published, and "N." could be an abbreviation for the Latin "Nova" [new] or "Nobis" [us], or German "Neue", indicating that the name of the species was new (Zhang et al. 2023e). Hopffer labeled many Hesperiidae specimens in MFNB that he could not identify with such new names, but most of his names remained unpublished. Such species were subsequently described by other authors, who sometimes kept or modified Hopffer's names, or proposed unrelated ones.

We found the specimen with the number 4969 in MFNB, shown in Fig. 60a with its labels. The specimen agrees well with the original description of *E. hopfferi* that we assembled from Plötz's key and translate as: "Forewing without a central band on the upper surface. Hindwing not marked with white above. The underside of the forewing is broadly white towards the inner margin and tornus. Above, the body and wing bases are covered with shiny blue and green overscaling. On the underside, the costal margin of the forewing nearly to the apex is reddish-white gray, the white spot [by the tornus] extends very narrowly through the middle cell to the costal margin. Hindwing white at the base by costal margin, otherwise brown with 2 darker crossbands" (Plötz 1881). Moreover, the published illustration of *Telegonus hopfferi* in Draudt (1921–1924), reproduced here as Fig. 60b, may be a copy of Plötz's unpublished (and lost) drawing t[afel]. 88 referenced in the original description and showing syntype(s) of *E. hopfferi*. Many Hesperiidae illustrations in Draudt (1921–1924), especially of obscure and recently described species, were not drawn from specimens, but from their illustrations in other sources, such as Plötz's unpublished drawings. The illustration and the specimen are similar to each other, not only in the details of wing patterns, but also in the way the specimen was spread. This specimen No. 4969 may be the specimen drawn by Plötz, whose drawing was copied in Draudt (1921–1924).

As a result of these investigations, we conclude that the specimen No. 4969 is a syntype of *E. hopfferi*. Its appearance and associated data agree with the original description, unpublished manuscript by the original author, and published early illustrations of this taxon. Moreover, because Plötz did not wish to use the name "phanaeus," likely coined by Hopffer for this new species, it seemed fitting to propose a name honoring Hopffer, who passed away in 1876. That is the year dated on Plötz's manuscript with the name *hopfferi*, which was absent from his earlier manuscript (1870, also in ZSMC) that was a list of Hesperiidae species (including unpublished ones) known to Plötz at the time. Finally, the taxonomic identity of this syntype is in agreement with the current and prior use of this name in nearly all primary literature sources (Draudt 1922; Evans 1952; Mielke 2005) because Mexican populations, where this syntype is from, have been associated with this name.

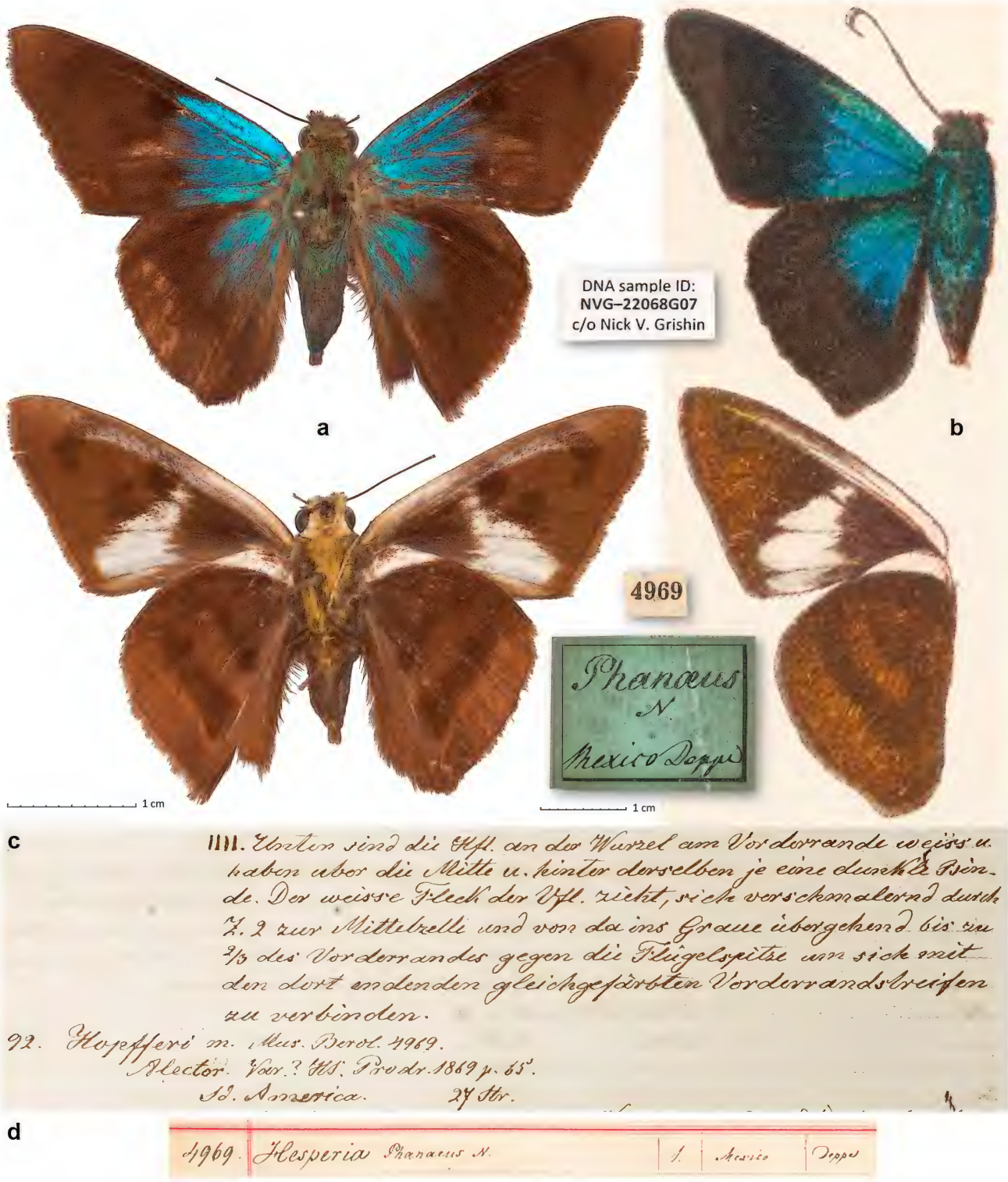
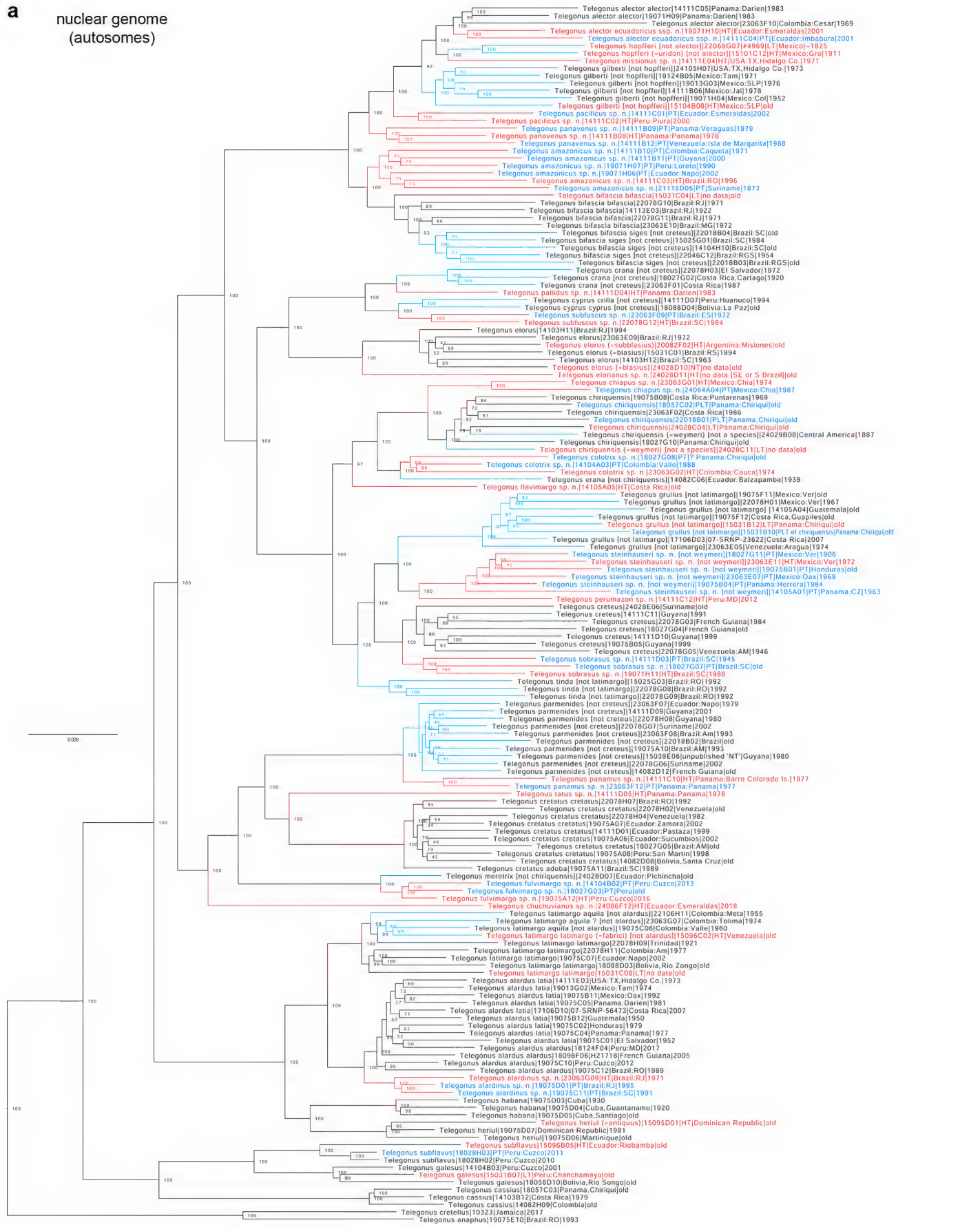
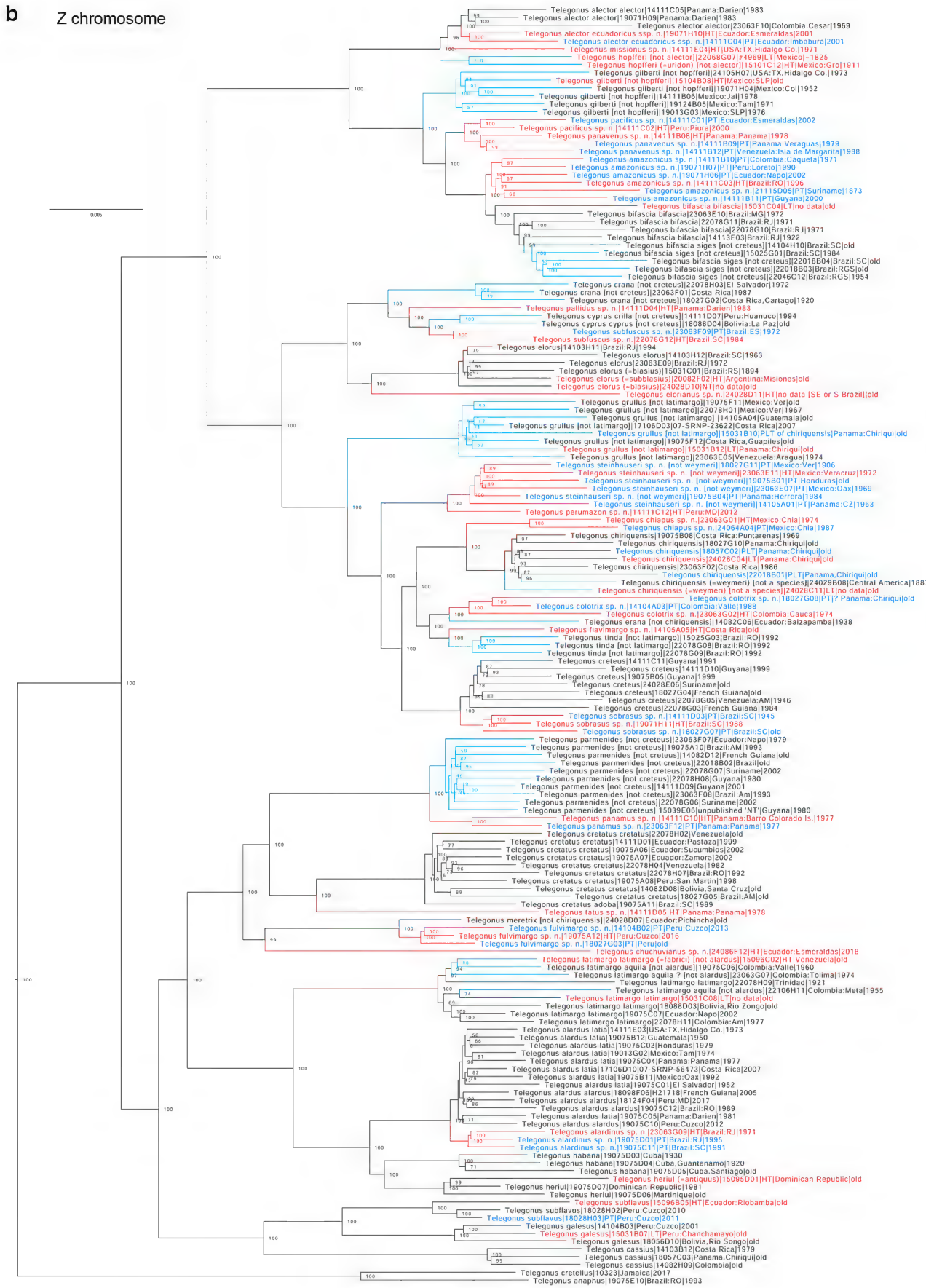

DNA sample ID:
NVG–22068G07
c/o Nick V. Grishin
a
b
4969
Phanaeus
N.
Mexico Dappe
1 cm
1 cm
c
IIII. Unten sind die Hfl. an der Wurzel am Vorderrande weiss u.
haben über die Mitte u. hinter derselben je eine dunkle Bin-
de. Der weisse Fleck der Vfl. zieht, sich verschmälernd durch
Z. 2 zur Mittelzelle und von da ins Graue übergehend bis zu
2/3 des Vorderrandes gegen die Flügelspitze um sich mit
den dort endenden gleichgefärbten Vorderrandsbinden
zu verbinden.
92. Hopfferi m. Mus. Berol. 4969.
Hector. Var.? Hfl. Prov. dr. 1869 p. 65.
Sd. America. 2½ Ithr.
d
4969 Hesperia Phanaeus N. 1 Mexico Dappe

Fig. 60. *Eudamus hopfferi* Plötz, 1881: **a)** the lectotype (designated herein) with its labels and **b)** illustrations from Draudt (1922: Pl. 167), which is likely a copy of an unpublished Plötz's drawing t. 88, in dorsal (above) and ventral (below) views; **c)** an excerpt with the description of *E. hopfferi* from Plötz's manuscript in ZSMC library dated 1876 that is an earlier version of his published works; **d)** a line for the No. 4969 in the MFNB collection catalog, written by Hopffer. Larger scale bar refers to the specimen, and smaller scale bar refers to labels, which are reduced by one-third compared to the specimen.


a
nuclear genome
(autosomes)
Telegonus alector alector|14111C05|Panama:Darien|1983
Telegonus alector alector|19071H09|Panama:Darien|1983
Telegonus alector alector|23063F10|Colombia:Cesar|1969
Telegonus alector ecuadoricus ssp. n.|19071H10|HT|Ecuador:Esmeraldas|2001
Telegonus alector ecuadoricus ssp. n.|14111C04|PT|Ecuador:Imbabura|2001
Telegonus hopfferi [not alector]|22068G07|#4969|LT|Mexico|~1825
Telegonus hopfferi (=uridon) [not alector]|15101C12|HT|Mexico:Gro|1911
Telegonus missionus sp. n.|14111E04|HT|USA:TX,Hidalgo Co.|1971
Telegonus gilberti [not hopfferi]|24105H07|USA:TX,Hidalgo Co.|1973
Telegonus gilberti [not hopfferi]|19124B05|Mexico:Tam|1971
Telegonus gilberti [not hopfferi]|19013G03|Mexico:SLP|1976
Telegonus gilberti [not hopfferi]|14111B06|Mexico:Jal|1978
Telegonus gilberti [not hopfferi]|19071H04|Mexico:Col|1952
Telegonus gilberti [not hopfferi]|15104B08|HT|Mexico:SLP|old
Telegonus pacificus sp. n.|14111C01|PT|Ecuador:Esmeraldas|2002
Telegonus pacificus sp. n.|14111C02|HT|Peru:Piura|2000
Telegonus panavenus sp. n.|14111B09|PT|Panama:Veraguas|1979
Telegonus panavenus sp. n.|14111B08|HT|Panama:Panama|1978
Telegonus panavenus sp. n.|14111B12|PT|Venezuela:Isla de Margarita|1988
Telegonus amazonicus sp. n.|14111B10|PT|Colombia:Caqueta|1971
Telegonus amazonicus sp. n.|14111B11|PT|Guyana|2000
Telegonus amazonicus sp. n.|19071H07|PT|Peru:Loreto|1990
Telegonus amazonicus sp. n.|19071H06|PT|Ecuador:Napo|2002
Telegonus amazonicus sp. n.|14111C03|HT|Brazil:RO|1996
Telegonus amazonicus sp. n.|21115D05|PT|Suriname|1873
Telegonus bifascia bifascia|15031C04|LT|no data|old
Telegonus bifascia bifascia|22078G10|Brazil:RJ|1971
Telegonus bifascia bifascia|14113E03|Brazil:RJ|1922
Telegonus bifascia bifascia|22078G11|Brazil:RJ|1971
Telegonus bifascia bifascia|23063E10|Brazil:MG|1972
Telegonus bifascia siges [not creteus]|22018B04|Brazil:SC|old
Telegonus bifascia siges [not creteus]|15025G01|Brazil:SC|1984
Telegonus bifascia siges [not creteus]|14104H10|Brazil:SC|old
Telegonus bifascia siges [not creteus]|22046C12|Brazil:RGS|1954
Telegonus bifascia siges [not creteus]|22018B03|Brazil:RGS|old
Telegonus crana [not creteus]|22078H03|El Salvador|1972
Telegonus crana [not creteus]|18027G02|Costa Rica,Cartago|1920
Telegonus crana [not creteus]|23063F01|Costa Rica|1987
Telegonus palliidus sp. n.|14111D04|HT|Panama:Darien|1983
Telegonus cyprus crilla [not creteus]|14111D07|Peru:Huanuco|1994
Telegonus cyprus cyprus [not creteus]|18088D04|Bolivia:La Paz|old
Telegonus subfuscus sp. n.|23063F09|PT|Brazil:ES|1972
Telegonus subfuscus sp. n.|22078G12|HT|Brazil:SC|1984
Telegonus elorus|14103H11|Brazil:RJ|1994
Telegonus elorus|23063E09|Brazil:RJ|1972
Telegonus elorus (=subblasius)|20082F02|HT|Argentina:Misiones|old
Telegonus elorus (=blasius)|15031C01|Brazil:RS|1894
Telegonus elorus|14103H12|Brazil:SC|1963
Telegonus elorus (=blasius)|24028D10|NT|no data|old
Telegonus elorianus sp. n.|24028D11|HT|no data [SE or S Brazil]|old
Telegonus chiapus sp. n.|23063G01|HT|Mexico:Chia|1974
Telegonus chiapus sp. n.|24064A04|PT|Mexico:Chia|1987
Telegonus chiriquensis|19075B08|Costa Rica:Puntarenas|1969
Telegonus chiriquensis|18057C02|PLT|Panama:Chiriqui|old
Telegonus chiriquensis|23063F02|Costa Rica|1986
Telegonus chiriquensis|22018B01|PLT|Panama,Chiriqui|old
Telegonus chiriquensis|24028C04|LT|Panama:Chiriqui|old
Telegonus chiriquensis (=weymeri) [not a species]|24029B08|Central America|1887
Telegonus chiriquensis|18027G10|Panama:Chiriqui|old
Telegonus chiriquensis (=weymeri) [not a species]|24028C11|LT|no data|old
Telegonus colotrix sp. n.|18027G08|PT|? Panama:Chiriqui|old
Telegonus colotrix sp. n.|14104A03|PT|Colombia:Valle|1988
Telegonus colotrix sp. n.|23063G02|HT|Colombia:Cauca|1974
Telegonus erana [not chiriquensis]|14082C06|Ecuador:Balzapamba|1938
Telegonus flavimargo sp. n.|14105A05|HT|Costa Rica|old
Telegonus grullus [not latimargo]|19075F11|Mexico:Ver|old
Telegonus grullus [not latimargo]|22078H01|Mexico:Ver|1967
Telegonus grullus [not latimargo] |14105A04|Guatemala|old
Telegonus grullus [not latimargo]|19075F12|Costa Rica,Guapiles|old
Telegonus grullus [not latimargo]|15031B12|LT|Panama:Chiriqui|old
Telegonus grullus [not latimargo]|15031B10|PLT of chiriquensis|Panama:Chiriqui|old
Telegonus grullus [not latimargo]|17106D03|07-SRNP-23622|Costa Rica|2007
Telegonus grullus [not latimargo]|23063E05|Venezuela:Aragua|1974
Telegonus steinhauseri sp. n. [not weymeri]|18027G11|PT|Mexico:Ver|1906
Telegonus steinhauseri sp. n. [not weymeri]|23063E11|HT|Mexico:Ver|1972
Telegonus steinhauseri sp. n. [not weymeri]|19075B01|PT|Honduras|old
Telegonus steinhauseri sp. n. [not weymeri]|23063E07|PT|Mexico:Oax|1969
Telegonus steinhauseri sp. n. [not weymeri]|19075B04|PT|Panama:Herrera|1984
Telegonus steinhauseri sp. n. [not weymeri]|14105A01|PT|Panama:CZ|1963
Telegonus perumazon sp. n.|14111C12|HT|Peru:MD|2012
Telegonus creteus|24028E06|Suriname|old
Telegonus creteus|14111C11|Guyana|1991
Telegonus creteus|22078G03|French Guiana|1984
Telegonus creteus|18027G04|French Guiana|old
Telegonus creteus|14111D10|Guyana|1999
Telegonus creteus|19075B05|Guyana|1999
Telegonus creteus|22078G05|Venezuela:AM|1946
Telegonus sobrasus sp. n.|14111D03|PT|Brazil:SC|1945
Telegonus sobrasus sp. n.|18027G07|PT|Brazil:SC|old
Telegonus sobrasus sp. n.|19071H11|HT|Brazil:SC|1988
Telegonus tinda [not latimargo]|15025G03|Brazil:RO|1992
Telegonus tinda [not latimargo]|22078G08|Brazil:RO|1992
Telegonus tinda [not latimargo]|22078G09|Brazil:RO|1992
Telegonus parmenides [not creteus]|23063F07|Ecuador:Napo|1979
Telegonus parmenides [not creteus]|14111D09|Guyana|2001
Telegonus parmenides [not creteus]|22078H08|Guyana|1980
Telegonus parmenides [not creteus]|22078G07|Suriname|2002
Telegonus parmenides [not creteus]|23063F08|Brazil:Am|1993
Telegonus parmenides [not creteus]|22018B02|Brazil|old
Telegonus parmenides [not creteus]|19075A10|Brazil:AM|1993
Telegonus parmenides [not creteus]|15039E06|unpublished 'NT'|Guyana|1980
Telegonus parmenides [not creteus]|22078G06|Suriname|2002
Telegonus parmenides [not creteus]|14082D12|French Guiana|old
Telegonus panamus sp. n.|14111C10|HT|Panama:Barro Colorado Is.|1977
Telegonus panamus sp. n.|23063F12|PT|Panama:Panama|1977
Telegonus tatus sp. n.|14111D05|HT|Panama:Panama|1978
Telegonus cretatus cretatus|22078H07|Brazil:RO|1992
Telegonus cretatus cretatus|22078H02|Venezuela|old
Telegonus cretatus cretatus|22078H04|Venezuela|1982
Telegonus cretatus cretatus|19075A07|Ecuador:Zamora|2002
Telegonus cretatus cretatus|14111D01|Ecuador:Pastaza|1999
Telegonus cretatus cretatus|19075A06|Ecuador:Sucumbios|2002
Telegonus cretatus cretatus|18027G05|Brazil:AM|old
Telegonus cretatus cretatus|19075A08|Peru:San Martin|1998
Telegonus cretatus cretatus|14082D08|Bolivia,Santa Cruz|old
Telegonus cretatus adoba|19075A11|Brazil:SC|1989
Telegonus meretrix [not chiriquensis]|24028D07|Ecuador:Pichincha|old
Telegonus fulvimargo sp. n.|14104B02|PT|Peru:Cuzco|2013
Telegonus fulvimargo sp. n.|18027G03|PT|Peru|old
Telegonus fulvimargo sp. n.|19075A12|HT|Peru:Cuzco|2016
Telegonus chuchuvianus sp. n.|24086F12|HT|Ecuador:Esmeraldas|2018
Telegonus latimargo aquila [not alardus]|22106H11|Colombia:Meta|1955
Telegonus latimargo aquila ? [not alardus]|23063G07|Colombia:Tolima|1974
Telegonus latimargo aquila [not alardus]|19075C06|Colombia:Valle|1960
Telegonus latimargo latimargo (=fabrici) [not alardus]|15096C02|HT|Venezuela|old
Telegonus latimargo latimargo|22078H09|Trinidad|1921
Telegonus latimargo latimargo|22078H11|Colombia:Am|1977
Telegonus latimargo latimargo|19075C07|Ecuador:Napo|2002
Telegonus latimargo latimargo|18088D03|Bolivia,Rio Zongo|old
Telegonus latimargo latimargo|15031C08|LT|no data|old
Telegonus alardus latia|14111E03|USA:TX,Hidalgo Co.|1973
Telegonus alardus latia|19013G02|Mexico:Tam|1974
Telegonus alardus latia|19075B11|Mexico:Oax|1992
Telegonus alardus latia|19075C05|Panama:Darien|1981
Telegonus alardus latia|17106D10|07-SRNP-56473|Costa Rica|2007
Telegonus alardus latia|19075B12|Guatemala|1950
Telegonus alardus latia|19075C02|Honduras|1979
Telegonus alardus latia|19075C04|Panama:Panama|1977
Telegonus alardus latia|19075C01|El Salvador|1952
Telegonus alardus alardus|18124F04|Peru:MD|2017
Telegonus alardus alardus|18098F06|H21718|French Guiana|2005
Telegonus alardus alardus|19075C10|Peru:Cuzco|2012
Telegonus alardus alardus|19075C12|Brazil:RO|1989
Telegonus alardinus sp. n.|23063G09|HT|Brazil:RJ|1971
Telegonus alardinus sp. n.|19075D01|PT|Brazil:RJ|1995
Telegonus alardinus sp. n.|19075C11|PT|Brazil:SC|1991
Telegonus habana|19075D03|Cuba|1930
Telegonus habana|19075D04|Cuba,Guantanamo|1920
Telegonus habana|19075D05|Cuba,Santiago|old
Telegonus heriul (=antiquus)|15095D01|HT|Dominican Republic|old
Telegonus heriul|19075D07|Dominican Republic|1981
Telegonus heriul|19075D06|Martinique|old
Telegonus subflavus|15096B03|HT|Ecuador:Riobamba|old
Telegonus subflavus|18028H03|PT|Peru:Cuzco|2011
Telegonus subflavus|18028H02|Peru:Cuzco|2010
Telegonus galesus|14104B03|Peru:Cuzco|2001
Telegonus galesus|15031B07|LT|Peru:Chanchamayo|old
Telegonus galesus|18056D10|Bolivia,Rio Songo|old
Telegonus cassius|18057C03|Panama,Chiriqui|old
Telegonus cassius|14103B12|Costa Rica|1979
Telegonus cassius|14082H09|Colombia|old
Telegonus cretellus|10323|Jamaica|2017
Telegonus anaphus|19075E10|Brazil:RO|1993
0.008


b
Z chromosome
0.005
Telegonus alector alector|14111C05|Panama:Darien|1983
Telegonus alector alector|19071H09|Panama:Darien|1983
Telegonus alector alector|23063F10|Colombia:Cesar|1969
Telegonus alector ecuadoricus ssp. n.|19071H10|HT|Ecuador:Esmeraldas|2001
Telegonus alector ecuadoricus ssp. n.|14111C04|PT|Ecuador:Imbabura|2001
Telegonus missionis sp. n.|14111E04|HT|USA:TX, Hidalgo Co.|1971
Telegonus hopfferi [not alector]|22068G07|#4969|LT|Mexico|~1825
Telegonus hopfferi (=uridon) [not alector]|15101C12|HT|Mexico:Gro|1911
Telegonus gilberti [not hopfferi]|24105H07|USA:TX, Hidalgo Co.|1973
Telegonus giberti [not hopfferi]|15104B08|HT|Mexico:SLP|old
Telegonus gilberti [not hopfferi]|19071H04|Mexico:Col|1952
Telegonus gilberti [not hopfferi]|14111B06|Mexico:Jal|1978
Telegonus gilberti [not hopfferi]|19124B05|Mexico:Tam|1971
Telegonus gilberti [not hopfferi]|19013G03|Mexico:SLP|1976
Telegonus pacificus sp. n.|14111C01|PT|Ecuador:Esmeraldas|2002
Telegonus pacificus sp. n.|14111C02|HT|Peru:Piura|2000
Telegonus panavenus sp. n.|14111B08|HT|Panama:Panama|1978
Telegonus panavenus sp. n.|14111B09|PT|Panama:Veraguas|1979
Telegonus panavenus sp. n.|14111B12|PT|Venezuela:Isla de Margarita|1988
Telegonus amazonicus sp. n.|14111B10|PT|Colombia:Caqueta|1971
Telegonus amazonicus sp. n.|19071H07|PT|Peru:Loreto|1990
Telegonus amazonicus sp. n.|19071H06|PT|Ecuador:Napo|2002
Telegonus amazonicus sp. n.|14111C03|HT|Brazil:RO|1996
Telegonus amazonicus sp. n.|21115D05|PT|Suriname|1873
Telegonus amazonicus sp. n.|14111B11|PT|Guyana|2000
Telegonus bifascia bifascia|15031C04|LT|no data|old
Telegonus bifascia bifascia|23063E10|Brazil:MG|1972
Telegonus bifascia bifascia|22078G11|Brazil:RJ|1971
Telegonus bifascia bifascia|22078G10|Brazil:RJ|1971
Telegonus bifascia bifascia|14113E03|Brazil:RJ|1922
Telegonus bifascia siges [not creteus]|14104H10|Brazil:SC|old
Telegonus bifascia siges [not creteus]|15025G01|Brazil:SC|1984
Telegonus bifascia siges [not creteus]|22018B04|Brazil:SC|old
Telegonus bifascia siges [not creteus]|22018B03|Brazil:RGS|old
Telegonus bifascia siges [not creteus]|22046C12|Brazil:RGS|1954
Telegonus crana [not creteus]|22078H03|El Salvador|1972
Telegonus crana [not creteus]|23063F01|Costa Rica|1987
Telegonus crana [not creteus]|18027G02|Costa Rica,Cartago|1920
Telegonus pallidus sp. n.|14111D04|HT|Panama:Darien|1983
Telegonus cyprus crilla [not creteus]|14111D07|Peru:Huanuco|1994
Telegonus cyprus cyprus [not creteus]|18088D04|Bolivia:La Paz|old
Telegonus subfuscus sp. n.|23063F09|PT|Brazil:ES|1972
Telegonus subfuscus sp. n.|22078G12|HT|Brazil:SC|1984
Telegonus elorus|14103H11|Brazil:RJ|1994
Telegonus elorus|14103H12|Brazil:SC|1963
Telegonus elorus|23063E09|Brazil:RJ|1972
Telegonus elorus (=blasius)|15031C01|Brazil:RS|1894
Telegonus elorus (=subblasius)|20082F02|HT|Argentina:Misiones|old
Telegonus elorus (=blasius)|24028D10|NT|no data|old
Telegonus elorianus sp. n.|24028D11|HT|no data [SE or S Brazil]|old
Telegonus grullus [not latimargo]|19075F11|Mexico:Ver|old
Telegonus grullus [not latimargo]|22078H01|Mexico:Ver|1967
Telegonus grullus [not latimargo] |14105A04|Guatemala|old
Telegonus grullus [not latimargo]|17106D03|07-SRNP-23622|Costa Rica|2007
Telegonus grullus [not latimargo]|15031B10|PLT of chiriquensis|Panama:Chiriqui|old
Telegonus grullus [not latimargo]|19075F12|Costa Rica,Guapiles|old
Telegonus grullus [not latimargo]|15031B12|LT|Panama:Chiriqui|old
Telegonus grullus [not latimargo]|23063E05|Venezuela:Aragua|1974
Telegonus steinhauseri sp. n. [not weymeri]|18027G11|PT|Mexico:Ver|1906
Telegonus steinhauseri sp. n. [not weymeri]|23063E11|HT|Mexico:Veracruz|1972
Telegonus steinhauseri sp. n. [not weymeri]|19075B01|PT|Honduras|old
Telegonus steinhauseri sp. n. [not weymeri]|23063E07|PT|Mexico:Oax|1969
Telegonus steinhauseri sp. n. [not weymeri]|19075B04|PT|Panama:Herrera|1984
Telegonus steinhauseri sp. n. [not weymeri]|14105A01|PT|Panama:CZ|1963
Telegonus perumazon sp. n.|14111C12|HT|Peru:MD|2012
Telegonus chiapus sp. n.|23063G01|HT|Mexico:Chia|1974
Telegonus chiapus sp. n.|24064A04|PT|Mexico:Chia|1987
Telegonus chiriquensis|19075B08|Costa Rica:Puntarenas|1969
Telegonus chiriquensis|18027G10|Panama:Chiriqui|old
Telegonus chiriquensis|18057C02|PLT|Panama:Chiriqui|old
Telegonus chiriquensis|24028C04|LT|Panama:Chiriqui|old
Telegonus chiriquensis|23063F02|Costa Rica|1986
Telegonus chiriquensis|22018B01|PLT|Panama,Chiriqui|old
Telegonus chiriquensis (=weymeri) [not a species]|24029B08|Central America|1887
Telegonus chiriquensis (=weymeri) [not a species]|24028C11|LT|no data|old
Telegonus colotrix sp. n.|18027G08|PT|? Panama:Chiriqui|old
Telegonus colotrix sp. n.|14104A03|PT|Colombia:Valle|1988
Telegonus colotrix sp. n.|23063G02|HT|Colombia:Cauca|1974
Telegonus erana [not chiriquensis]|14082C06|Ecuador:Balzapamba|1938
Telegonus flavimargo sp. n.|14105A05|HT|Costa Rica|old
Telegonus tinda [not latimargo]|15025G03|Brazil:RO|1992
Telegonus tinda [not latimargo]|22078G08|Brazil:RO|1992
Telegonus tinda [not latimargo]|22078G09|Brazil:RO|1992
Telegonus creteus|14111C11|Guyana|1991
Telegonus creteus|14111D10|Guyana|1999
Telegonus creteus|19075B05|Guyana|1999
Telegonus creteus|24028E06|Suriname|old
Telegonus creteus|18027G04|French Guiana|old
Telegonus creteus|22078G05|Venezuela:AM|1946
Telegonus creteus|22078G03|French Guiana|1984
Telegonus sobrasus sp. n.|14111D03|PT|Brazil:SC|1945
Telegonus sobrasus sp. n.|19071H11|HT|Brazil:SC|1988
Telegonus sobrasus sp. n.|18027G07|PT|Brazil:SC|old
Telegonus parmenides [not creteus]|23063F07|Ecuador:Napo|1979
Telegonus parmenides [not creteus]|19075A10|Brazil:AM|1993
Telegonus parmenides [not creteus]|14082D12|French Guiana|old
Telegonus parmenides [not creteus]|22018B02|Brazil|old
Telegonus parmenides [not creteus]|22078G07|Suriname|2002
Telegonus parmenides [not creteus]|22078H08|Guyana|1980
Telegonus parmenides [not creteus]|14111D09|Guyana|2001
Telegonus parmenides [not creteus]|23063F08|Brazil:Am|1993
Telegonus parmenides [not creteus]|22078G06|Suriname|2002
Telegonus parmenides [not creteus]|15039E06|unpublished 'NT'|Guyana|1980
Telegonus panamus sp. n.|14111C10|HT|Panama:Barro Colorado Is.|1977
Telegonus panamus sp. n.|23063F12|PT|Panama:Panama|1977
Telegonus cretatus cretatus|22078H02|Venezuela|old
Telegonus cretatus cretatus|14111D01|Ecuador:Pastaza|1999
Telegonus cretatus cretatus|19075A06|Ecuador:Sucumbios|2002
Telegonus cretatus cretatus|19075A07|Ecuador:Zamora|2002
Telegonus cretatus cretatus|22078H04|Venezuela|1982
Telegonus cretatus cretatus|22078H07|Brazil:RO|1992
Telegonus cretatus cretatus|19075A08|Peru:San Martin|1998
Telegonus cretatus cretatus|14082D08|Bolivia,Santa Cruz|old
Telegonus cretatus cretatus|18027G05|Brazil:AM|old
Telegonus cretatus adoba|19075A11|Brazil:SC|1989
Telegonus tatus sp. n.|14111D05|HT|Panama:Panama|1978
Telegonus meretrix [not chiriquensis]|24028D07|Ecuador:Pichincha|old
Telegonus fulvimargo sp. n.|14104B02|PT|Peru:Cuzco|2013
Telegonus fulvimargo sp. n.|19075A12|HT|Peru:Cuzco|2016
Telegonus fulvimargo sp. n.|18027G03|PT|Peru|old
Telegonus chuchuvianus sp. n.|24086F12|HT|Ecuador:Esmeraldas|2018
Telegonus latimargo latimargo (=fabrici) [not alardus]|15096C02|HT|Venezuela|old
Telegonus latimargo aquila [not alardus]|19075C06|Colombia:Valle|1960
Telegonus latimargo aquila ? [not alardus]|23063G07|Colombia:Tolima|1974
Telegonus latimargo latimargo|22078H09|Trinidad|1921
Telegonus latimargo aquila [not alardus]|22106H11|Colombia:Meta|1955
Telegonus latimargo latimargo|15031C08|LT|no data|old
Telegonus latimargo latimargo|18088D03|Bolivia,Rio Zongo|old
Telegonus latimargo latimargo|19075C07|Ecuador:Napo|2002
Telegonus latimargo latimargo|22078H11|Colombia:Am|1977
Telegonus alardus latia|14111E03|USA:TX,Hidalgo Co.|1973
Telegonus alardus latia|19075B12|Guatemala|1950
Telegonus alardus latia|19075C02|Honduras|1979
Telegonus alardus latia|19013G02|Mexico:Tam|1974
Telegonus alardus latia|19075C04|Panama:Panama|1977
Telegonus alardus latia|17106D10|07-SRNP-56473|Costa Rica|2007
Telegonus alardus latia|19075B11|Mexico:Oax|1992
Telegonus alardus latia|19075C01|El Salvador|1952
Telegonus alardus alardus|18098F06|H21718|French Guiana|2005
Telegonus alardus alardus|18124F04|Peru:MD|2017
Telegonus alardus alardus|19075C12|Brazil:RO|1989
Telegonus alardus latia|19075C05|Panama:Darien|1981
Telegonus alardus alardus|19075C10|Peru:Cuzco|2012
Telegonus alardinus sp. n.|23063G09|HT|Brazil:RJ|1971
Telegonus alardinus sp. n.|19075D01|PT|Brazil:RJ|1995
Telegonus alardinus sp. n.|19075C11|PT|Brazil:SC|1991
Telegonus habana|19075D03|Cuba|1930
Telegonus habana|19075D04|Cuba,Guantanamo|1920
Telegonus habana|19075D05|Cuba,Santiago|old
Telegonus heriul (=antiquus)|15095D01|HT|Dominican Republic|old
Telegonus heriul|19075D07|Dominican Republic|1981
Telegonus heriul|19075D06|Martinique|old
Telegonus subflavus|15096B05|HT|Ecuador:Riobamba|old
Telegonus subflavus|18028H02|Peru:Cuzco|2010
Telegonus subflavus|18028H03|PT|Peru:Cuzco|2011
Telegonus galesus|14104B03|Peru:Cuzco|2001
Telegonus galesus|15031B07|LT|Peru:Chanchamayo|old
Telegonus galesus|18056D10|Bolivia,Rio Songo|old
Telegonus cassius|14103B12|Costa Rica|1979
Telegonus cassius|18057C03|Panama,Chiriqui|old
Telegonus cassius|14082H09|Colombia|old
Telegonus cretellus|10323|Jamaica|2017
Telegonus anaphus|19075E10|Brazil:RO|1993

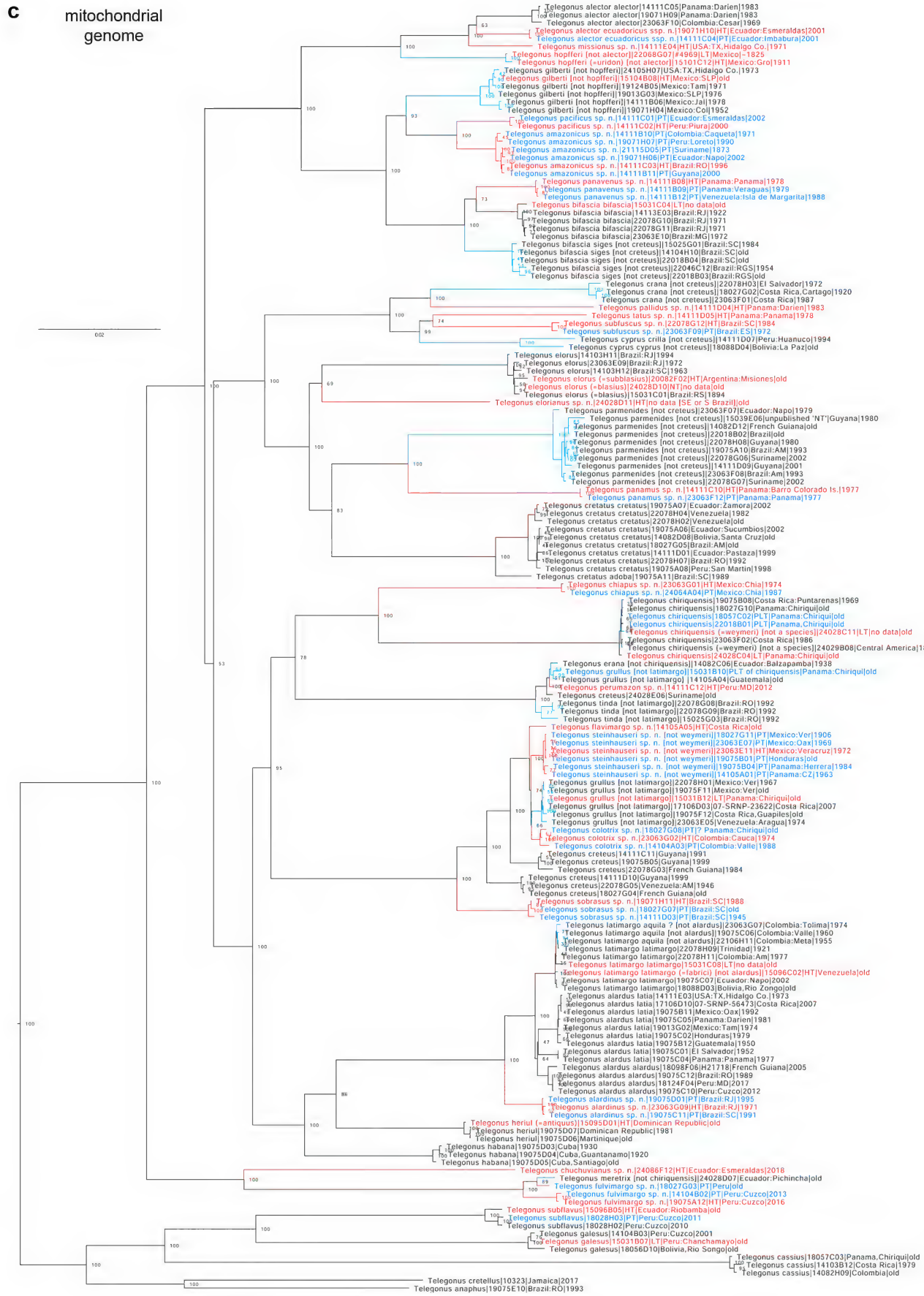

c
mitochondrial genome
0.02
Telegonus alector alector|14111C05|Panama:Darien|1983
Telegonus alector alector|19071H09|Panama:Darien|1983
Telegonus alector alector|23063F10|Colombia:Cesar|1969
Telegonus alector ecuadoricus ssp. n.|19071H10|HT|Ecuador:Esmeraldas|2001
Telegonus alector ecuadoricus ssp. n.|14111C04|PT|Ecuador:Imbabura|2001
Telegonus missionus sp. n.|14111E04|HT|USA:TX,Hidalgo Co.|1971
Telegonus hopfferi [not alector]|22068G07|#4969|LT|Mexico|~1825
Telegonus hopfferi (=uridon) [not alector]|15101C12|HT|Mexico:Gro|1911
Telegonus gilberti [not hopfferi]|24105H07|USA:TX,Hidalgo Co.|1973
Telegonus gilberti [not hopfferi]|15104B08|HT|Mexico:SLP|old
Telegonus gilberti [not hopfferi]|19124B05|Mexico:Tam|1971
Telegonus gilberti [not hopfferi]|19013G03|Mexico:SLP|1976
Telegonus gilberti [not hopfferi]|14111B06|Mexico:Jal|1978
Telegonus gilberti [not hopfferi]|19071H04|Mexico:Col|1952
Telegonus pacificus sp. n.|14111C01|PT|Ecuador:Esmeraldas|2002
Telegonus pacificus sp. n.|14111C02|HT|Peru:Piura|2000
Telegonus amazonicus sp. n.|14111B10|PT|Colombia:Caqueta|1971
Telegonus amazonicus sp. n.|19071H07|PT|Peru:Loreto|1990
Telegonus amazonicus sp. n.|21115D05|PT|Suriname|1873
Telegonus amazonicus sp. n.|19071H06|PT|Ecuador:Napo|2002
Telegonus amazonicus sp. n.|14111C03|HT|Brazil:RO|1996
Telegonus amazonicus sp. n.|14111B11|PT|Guyana|2000
Telegonus panavenus sp. n.|14111B08|HT|Panama:Panama|1978
Telegonus panavenus sp. n.|14111B09|PT|Panama:Veraguas|1979
Telegonus panavenus sp. n.|14111B12|PT|Venezuela:Isla de Margarita|1988
Telegonus bifascia bifascia|15031C04|LT|no data|old
Telegonus bifascia bifascia|14113E03|Brazil:RJ|1922
Telegonus bifascia bifascia|22078G10|Brazil:RJ|1971
Telegonus bifascia bifascia|22078G11|Brazil:RJ|1971
Telegonus bifascia bifascia|23063E10|Brazil:MG|1972
Telegonus bifascia siges [not creteus]|15025G01|Brazil:SC|1984
Telegonus bifascia siges [not creteus]|14104H10|Brazil:SC|old
Telegonus bifascia siges [not creteus]|22018B04|Brazil:SC|old
Telegonus bifascia siges [not creteus]|22046C12|Brazil:RGS|1954
Telegonus bifascia siges [not creteus]|22018B03|Brazil:RGS|old
Telegonus crana [not creteus]|22078H03|El Salvador|1972
Telegonus crana [not creteus]|18027G02|Costa Rica,Cartago|1920
Telegonus crana [not creteus]|23063F01|Costa Rica|1987
Telegonus pallidus sp. n.|14111D04|HT|Panama:Darien|1983
Telegonus latus sp. n.|14111D05|HT|Panama:Panama|1978
Telegonus subfuscus sp. n.|22078G12|HT|Brazil:SC|1984
Telegonus subfuscus sp. n.|23063F09|PT|Brazil:ES|1972
Telegonus cyprus crilla [not creteus]|14111D07|Peru:Huanuco|1994
Telegonus cyprus cyprus [not creteus]|18088D04|Bolivia:La Paz|old
Telegonus elorus|14103H11|Brazil:RJ|1994
Telegonus elorus|23063E09|Brazil:RJ|1972
Telegonus elorus|14103H12|Brazil:SC|1963
Telegonus elorus (=subblasius)|20082F02|HT|Argentina:Misiones|old
Telegonus elorus (=blasius)|24028D10|NT|no data|old
Telegonus elorus (=blasius)|15031C01|Brazil:RS|1894
Telegonus elorianus sp. n.|24028D11|HT|no data |SE or S Brazil|old
Telegonus parmenides [not creteus]|23063F07|Ecuador:Napo|1979
Telegonus parmenides [not creteus]|15039E06|unpublished 'NT'|Guyana|1980
Telegonus parmenides [not creteus]|14082D12|French Guiana|old
Telegonus parmenides [not creteus]|22018B02|Brazil|old
Telegonus parmenides [not creteus]|22078H08|Guyana|1980
Telegonus parmenides [not creteus]|19075A10|Brazil:AM|1993
Telegonus parmenides [not creteus]|22078G06|Suriname|2002
Telegonus parmenides [not creteus]|14111D09|Guyana|2001
Telegonus parmenides [not creteus]|23063F08|Brazil:Am|1993
Telegonus parmenides [not creteus]|22078G07|Suriname|2002
Telegonus panamus sp. n.|14111C10|HT|Panama:Barro Colorado Is.|1977
Telegonus panamus sp. n.|23063F12|PT|Panama:Panama|1977
Telegonus cretatus cretatus|19075A07|Ecuador:Zamora|2002
Telegonus cretatus cretatus|22078H04|Venezuela|1982
Telegonus cretatus cretatus|22078H02|Venezuela|old
Telegonus cretatus cretatus|19075A06|Ecuador:Sucumbios|2002
Telegonus cretatus cretatus|14082D08|Bolivia,Santa Cruz|old
Telegonus cretatus cretatus|18027G05|Brazil:AM|old
Telegonus cretatus cretatus|14111D01|Ecuador:Pastaza|1999
Telegonus cretatus cretatus|22078H07|Brazil:RO|1992
Telegonus cretatus cretatus|19075A08|Peru:San Martin|1998
Telegonus cretatus adoba|19075A11|Brazil:SC|1989
Telegonus chiapus sp. n.|23063G01|HT|Mexico:Chia|1974
Telegonus chiapus sp. n.|24064A04|PT|Mexico:Chia|1987
Telegonus chiriquensis|19075B08|Costa Rica:Puntarenas|1969
Telegonus chiriquensis|18027G10|Panama:Chiriqui|old
Telegonus chiriquensis|18057C02|PLT|Panama:Chiriqui|old
Telegonus chiriquensis|22018B01|PLT|Panama,Chiriqui|old
Telegonus chiriquensis (=weymeri) [not a species]|24028C11|LT|no data|old
Telegonus chiriquensis|23063F02|Costa Rica|1986
Telegonus chiriquensis (=weymeri) [not a species]|24029B08|Central America|1887
Telegonus chiriquensis|24028C04|LT|Panama:Chiriqui|old
Telegonus erana [not chiriquensis]|14082C06|Ecuador:Balzapamba|1938
Telegonus grullus [not latimargo]|15031B10|PLT of chiriquensis|Panama:Chiriqui|old
Telegonus grullus [not latimargo] |14105A04|Guatemala|old
Telegonus perumazon sp. n.|14111C12|HT|Peru:MD|2012
Telegonus creteus|24028E06|Suriname|old
Telegonus tinda [not latimargo]|22078G08|Brazil:RO|1992
Telegonus tinda [not latimargo]|22078G09|Brazil:RO|1992
Telegonus tinda [not latimargo]|15025G03|Brazil:RO|1992
Telegonus flavimargo sp. n.|14105A05|HT|Costa Rica|old
Telegonus steinhauseri sp. n. [not weymeri]|18027G11|PT|Mexico:Ver|1906
Telegonus steinhauseri sp. n. [not weymeri]|23063E07|PT|Mexico:Oax|1969
Telegonus steinhauseri sp. n. [not weymeri]|23063E11|HT|Mexico:Veracruz|1972
Telegonus steinhauseri sp. n. [not weymeri]|19075B01|PT|Honduras|old
Telegonus steinhauseri sp. n. [not weymeri]|19075B04|PT|Panama:Herrera|1984
Telegonus steinhauseri sp. n. [not weymeri]|14105A01|PT|Panama:CZ|1963
Telegonus grullus [not latimargo]|22078H01|Mexico:Ver|1967
Telegonus grullus [not latimargo]|19075F11|Mexico:Ver|old
Telegonus grullus [not latimargo]|15031B12|LT|Panama:Chiriqui|old
Telegonus grullus [not latimargo]|17106D03|07-SRNP-23622|Costa Rica|2007
Telegonus grullus [not latimargo]|19075F12|Costa Rica,Guapiles|old
Telegonus grullus [not latimargo]|23063E05|Venezuela:Aragua|1974
Telegonus colotrix sp. n.|18027G08|PT|? Panama:Chiriqui|old
Telegonus colotrix sp. n.|23063G02|HT|Colombia:Cauca|1974
Telegonus colotrix sp. n.|14104A03|PT|Colombia:Valle|1988
Telegonus creteus|14111C11|Guyana|1991
Telegonus creteus|19075B05|Guyana|1999
Telegonus creteus|22078G03|French Guiana|1984
Telegonus creteus|14111D10|Guyana|1999
Telegonus creteus|22078G05|Venezuela:AM|1946
Telegonus creteus|18027G04|French Guiana|old
Telegonus sobrasus sp. n.|19071H11|HT|Brazil:SC|1988
Telegonus sobrasus sp. n.|18027G07|PT|Brazil:SC|old
Telegonus sobrasus sp. n.|14111D03|PT|Brazil:SC|1945
Telegonus latimargo aquila ? [not alardus]|23063G07|Colombia:Tolima|1974
Telegonus latimargo aquila [not alardus]|19075C06|Colombia:Valle|1960
Telegonus latimargo aquila [not alardus]|22106H11|Colombia:Meta|1955
Telegonus latimargo latimargo|22078H09|Trinidad|1921
Telegonus latimargo latimargo|22078H11|Colombia:Am|1977
Telegonus latimargo latimargo|15031C08|LT|no data|old
Telegonus latimargo latimargo (=fabrici) [not alardus]|15096C02|HT|Venezuela|old
Telegonus latimargo latimargo|19075C07|Ecuador:Napo|2002
Telegonus latimargo latimargo|18088D03|Bolivia,Rio Zongo|old
Telegonus alardus latia|14111E03|USA:TX,Hidalgo Co.|1973
Telegonus alardus latia|17106D10|07-SRNP-56473|Costa Rica|2007
Telegonus alardus latia|19075B11|Mexico:Oax|1992
Telegonus alardus latia|19075C05|Panama:Darien|1981
Telegonus alardus latia|19013G02|Mexico:Tam|1974
Telegonus alardus latia|19075C02|Honduras|1979
Telegonus alardus latia|19075B12|Guatemala|1950
Telegonus alardus latia|19075C01|El Salvador|1952
Telegonus alardus latia|19075C04|Panama:Panama|1977
Telegonus alardus alardus|18098F06|H21718|French Guiana|2005
Telegonus alardus alardus|19075C12|Brazil:RO|1989
Telegonus alardus alardus|18124F04|Peru:MD|2017
Telegonus alardus alardus|19075C10|Peru:Cuzco|2012
Telegonus alardinus sp. n.|19075D01|PT|Brazil:RJ|1995
Telegonus alardinus sp. n.|23063G09|HT|Brazil:RJ|1971
Telegonus alardinus sp. n.|19075C11|PT|Brazil:SC|1991
Telegonus heriul (=antiguus)|15095D01|HT|Dominican Republic|old
Telegonus heriul|19075D07|Dominican Republic|1981
Telegonus heriul|19075D06|Martinique|old
Telegonus habana|19075D03|Cuba|1930
Telegonus habana|19075D04|Cuba,Guantanamo|1920
Telegonus habana|19075D05|Cuba,Santiago|old
Telegonus chuchuvianus sp. n.|24086F12|HT|Ecuador:Esmeraldas|2018
Telegonus meretrix [not chiriquensis]|24028D07|Ecuador:Pichincha|old
Telegonus fulvimargo sp. n.|18027G03|PT|Peru|old
Telegonus fulvimargo sp. n.|14104B02|PT|Peru:Cuzco|2013
Telegonus fulvimargo sp. n.|19075A12|HT|Peru:Cuzco|2016
Telegonus subflavus|15096B05|HT|Ecuador:Riobamba|old
Telegonus subflavus|18028H03|PT|Peru:Cuzco|2011
Telegonus subflavus|18028H02|Peru:Cuzco|2010
Telegonus galesus|14104B03|Peru:Cuzco|2001
Telegonus galesus|15031B07|LT|Peru:Chanchamayo|old
Telegonus galesus|18056D10|Bolivia,Rio Songo|old
Telegonus cassius|18057C03|Panama,Chiriqui|old
Telegonus cassius|14103B12|Costa Rica|1979
Telegonus cassius|14082H09|Colombia|old
Telegonus cretellus|10323|Jamaica|2017
Telegonus anaphus|19075E10|Brazil:RO|1993

Fig. 61 (see previous 3 pages). Phylogenetic trees of *Telegonus* specimens analyzed in this work inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,285,392 positions, **b)** the Z chromosome, based on 358,395 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Primary and secondary type specimens are labeled in red and blue, respectively. Branches of new taxa proposed in this work are shown in red and those with taxonomic changes, such as subspecies-to-species or synonym-to-species status or transfer of a subspecies between species (changes indicated in brackets) are shown in blue.

To define the taxonomic identity of the name *E. hopfferi* objectively, N.V.G. hereby designates a syntype in the MFNB collection illustrated in Fig. 60a, a male with the following three labels (2nd handwritten and green, others printed and white): [4969], [Phanæus | N. | Mexico Deppe], and [DNA sample ID: | NVG-22068G07 | c/o Nick V. Grishin] as the **lectotype** of *Eudamus hopfferi* Plötz, 1881. The lectotype is missing the tornus of the right hindwing. The COI barcode sequence of the lectotype, sample NVG-22068G07, GenBank PV550009, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGACTTTTACCTCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGGACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAGCATCTGTTGACTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTCTTGGAGCTATTAATTTTATCACAACAATTATTAATATACGAATTAATAGTTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCTTTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATACCAACACTTATTT

As a result of the lectotype designation, the type locality of *Eudamus hopfferi* becomes Mexico, possibly in south-central or southern Mexico (states of Mexico, Puebla, Oaxaca, and around, but not more eastern territories, such as Veracruz), judging from Deppe's travels (Stresemann 1954) and genomic sequence comparison that also confirms *Thracides uridon* Dyar, 1912 (type locality in Mexico: Guerrero, holotype sequenced as NVG-15101C12) as a junior subjective synonym of *E. hopfferi* (Fig. 61).

Finally, it remains unclear why Plötz gave the locality of *E. hopfferi* as South America even in the original manuscript that listed the Mexican specimen by its number 4969 (Fig. 60c). It could have been that the locality referred to Herrich-Schäffer specimen(s)—the locality is given in the same line with the reference to them (Plötz 1881), some other specimen(s) Plötz inspected, or it may be an error.

Telegonus hopfferi (Plötz, 1881) is a species distinct from *Telegonus alector* (C. Felder & R. Felder, 1867)

Genomic analysis reveals that *Eudamus hopfferi* Plötz, 1881 (type locality in Mexico, likely south-central or southern, lectotype sequenced as NVG-22068G07), currently treated as a subspecies of *Telegonus alector* (C. Felder & R. Felder, 1867) (type locality Colombia: Bogota), is genetically differentiated from it at the species level (Fig. 61) with F_{st}/COI barcode difference of 0.32/1.7% (11 bp). Therefore, we propose that *Telegonus hopfferi* (Plötz, 1881), **stat. rest.** is a species distinct from *Telegonus alector* (C. Felder & R. Felder, 1867).

Telegonus (*Rhabdoides*) *alector ecuadoricus* Grishin, new subspecies

http://zoobank.org/2CAECE29-3F03-40DC-9A82-8D56D3940278

(Figs. 61 part, 62, 63a–b, 89 part)

Definition and diagnosis. Genomic analysis reveals that two specimens from Ecuador, while being closely related to *Telegonus alector* (C. Felder & R. Felder, 1867) (type locality Colombia: Bogota) are genetically differentiated from it and form a clade sister to *T. alector* from Panama, Colombia and Venezuela (Fig. 61), although this differentiation is small. Their COI barcodes differ by 1.1% (7 bp). This barcode difference is larger than expected from nuclear genomic divergence (Fig. 61) and, therefore, this new taxon is conservatively proposed as a subspecies. This new subspecies keys to "*Astraptes alector alector*" C.14.26(b) in Evans (1952) and is similar to it in having brilliant blue (not greenish) wing bases and body above, and a white central band on the forewing in males. It differs from the nominate subspecies by its males with a more weakly expressed white central band on the dorsal forewing, which is heavier overscaled with brown, and its portion in the discal cell is very much reduced; a more prominent white costal area on the ventral forewing that reaches nearly half of the wing from the base; and a more

Fig. 62. *Telegonus* (*Rhabdoides*) *alector ecuadoricus* **ssp. n.** holotype ♂ NVG-19071H10 in dorsal (left) and ventral (right) views.

strongly developed dark ventral wing pattern, including forewing subapical band and hindwing bands. In DNA, a combination of the following base pairs is diagnostic in the nuclear genome: aly294.13.1:T424A, aly294.13.1:T501A, aly3507.2.7:C39T, aly3507.2.7:A113C, aly322.20.17:C99T; and COI barcode: A43T, C136C, G477A, A517A, T568C, T646C.

Barcode sequence of the holotype. Sample NVG-19071H10, GenBank PV550010, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGTACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCTGGATCTTTAATTGGAGATGATCAAATTTACAATACT
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGACTTAGCAATTTTCTCTTTACATTTAGCTGGTATTTCTTCTATTCTTGGAGCTATTAATTTTATCACAACAATTATTAATATACGAATTAATAATCTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATCACAGCATTATTATTATTACTTTCTTTACCAGTTTTAGCAGGAGCCATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATACCAACACTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 62 (genitalia Fig. 63a, b), bears the following six printed rectangular labels, five white: [ECUADOR: Esmeraldas: | Río Chuchuví, km. 12.5 Lita- | San Lorenzo rd. 800-900m | 0° 53.01' N 78° 30.90' W | III.2001 I.Aldas leg.], [DNA sample ID: | NVG-19071H10 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E04 | c/o Nick V. Grishin], [genitalia: | NVG240817-43 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01588533], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | alector ecuadoricus | Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratype:** 1♂ NVG-14111C04 Ecuador, Imbabura, Rumiñahui, 37 km N of Pedro Vicente Maldonado, elevation 500 m, GPS 0.2788, −78.9983, Apr-2001, I. Aldas leg. [USNM].

Type locality. Ecuador: Esmeraldas Province, Río Chuchuví, km 12.5 of Lita–San Lorenzo Road, elevation 800-900 m, GPS 0.8835, −78.5150.

Etymology. The name is given for the type locality and is treated as a masculine noun in apposition.

Distribution. Currently known only from northwestern Ecuador.

Telegonus gilberti (H. Freeman, 1969) is a species distinct from *Telegonus hopfferi* (Plötz, 1881)

Genomic analysis reveals that *Astraptes gilberti* H. Freeman, 1969 (type locality in Mexico, San Luis Potosí, holotype sequenced as NVG-15104B08), currently regarded as a junior subjective synonym of *Telegonus hopfferi* (Plötz, 1881), **stat. rest.** (type locality in Mexico, likely south-central or southern, lectotype sequenced as NVG-22068G07), is in a different clade from several species of *Telegonus* Hübner, [1819] (type species *Papilio talus* Cramer, 1777) that include also *Telegonus alector* (C. Felder & R. Felder, 1867) (type locality Colombia: Bogota) (Fig. 61), and is prominently differentiated from *T. hopfferi* genetically; e.g., COI barcode difference of 2.6% (17 bp). Therefore, we propose that *Telegonus*

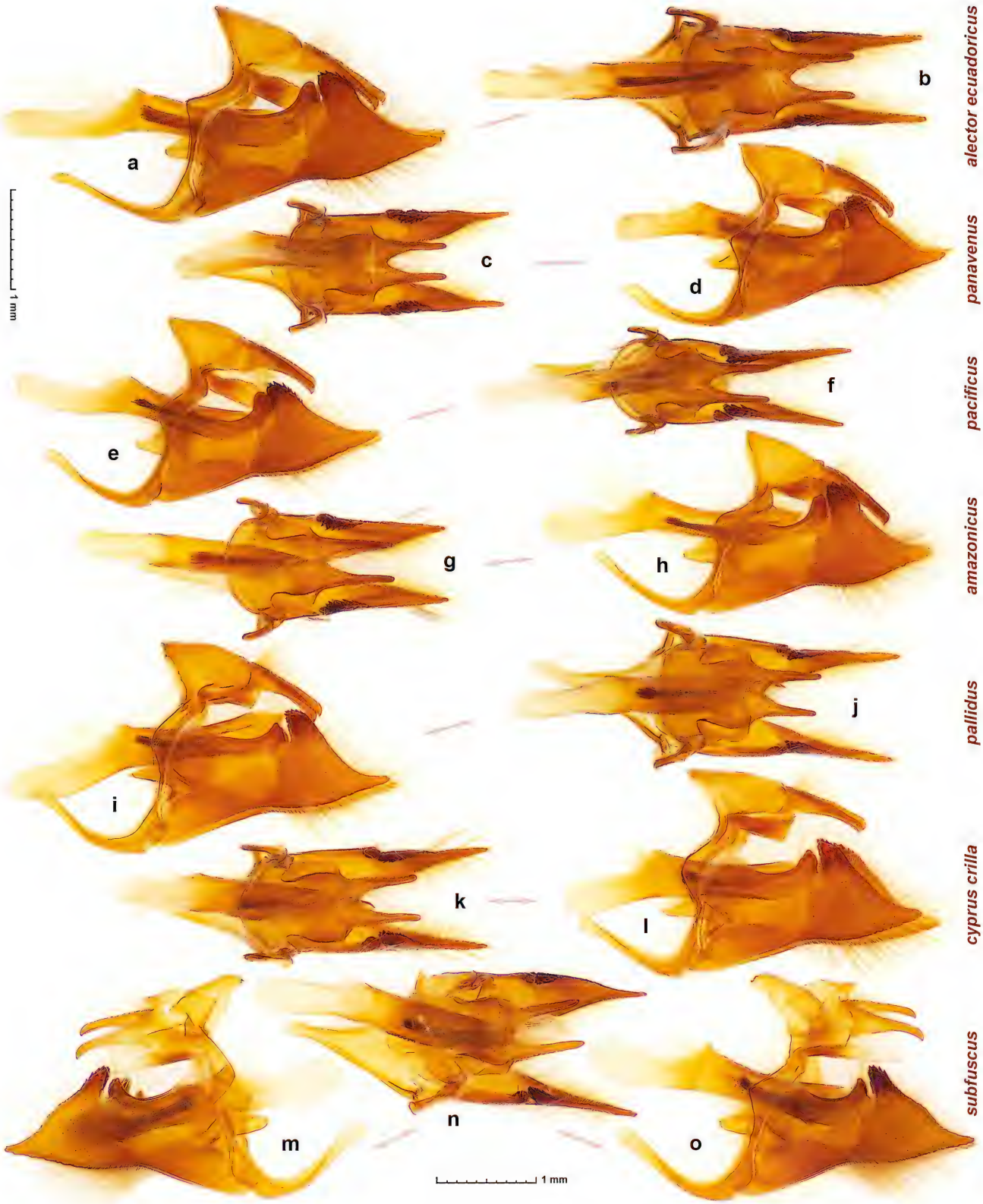


Fig. 63. Male genitalia of *Telegonus* (*Rhabdoides*) holotypes (unless indicated), data in text or below: **a–b)** *T. alector ecuadoricus* **ssp. n.** NVG-19071H10; **c–d)** *T. panavenus* **sp. n.** paratype NVG-14111B09; **e–f)** *T. pacificus* **sp. n.** NVG-14111C02; **g–h)** *T. amazonicus* **sp. n.** NVG-14111C03; **i–j)** *T. pallidus* **sp. n.** NVG-14111D04; **k–l)** *T. cyprus crilla* **comb. nov.** specimen NVG-14111D07 from Peru, Huanuco, Tingo Maria, 800 m, May-Jun-1994 [USNM]; **m–o)** *T. subfuscus* **sp. n.** NVG-22078G12 in different views: **a**, **d**, **e**, **h**, **i**, **l**, **o)** left lateral; **b**, **c**, **f**, **g**, **j**, **k**, **n)** dorsal; **m)** right lateral. The complete genital capsule is shown. Beige arrows connect different views of the same genitalia.

gilberti (Freeman, 1969), **stat. rest.** is a species distinct from *Telegonus hopfferi* (Plötz, 1881), **stat. rest.** Judging from the specimens we sequenced, *T. gilberti* ranges from the Río Grande Valley in Texas (USA) through Tamaulipas and Jalisco (Mexico) to Costa Rica.

Telegonus (*Rhabdoides*) *missionus* Grishin, new species

http://zoobank.org/BCC4198A-DEBB-48F6-8713-4FECEEF105C9

(Figs. 61 part, 64, 89 part)

Definition and diagnosis. Genomic analysis reveals that a specimen from the lower Río Grande Valley in Texas, USA, identified as *Telegonus hopfferi* (Plötz, 1881) (type locality in Mexico, likely south-central or southern, lectotype sequenced as NVG-22068G07) is genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 1.7% (11 bp), which is the same as the difference between *T. hopfferi* and *Telegonus alector* (C. Felder & R. Felder, 1867) (type locality Colombia: Bogota). This new species keys to "*Astraptes alector hopfferi*" C.14.26(a) in Evans (1952) but differs from it by being darker beneath, with a smaller ventral forewing pale tornal area that is overscaled with brown and does not reach the discal cell, reduced pale overscaling along the forewing costa typical of *T. hopfferi*, and a basal white triangle on the ventral hindwing that is partly overscaled with brown and with a less sharp and more diffuse edge separating it from the brown ground color. Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly671.37.7:A72C, aly671.37.7:T75C, aly3512.7.2:T60C, aly172.6.16:T36C, aly29286.1.3:G96A, aly60.18.6:C48C (not T), aly412.4.19:G108G (not A), aly216.44.7:C159C (not T), aly390.23.3:G60G (not C), aly378.37.11:G96G (not C); and COI barcode: A43T, T85C, C271T, A289G, A322A, A466G, T646T.

Barcode sequence of the holotype. Sample NVG-14111E04, GenBank PV550011, 658 base pairs:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGTACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCCGGATCTTTAATTGGAGATGATCAAATTTACAATACT
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCTCCATCATTAACTTTATTGATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGACTTAGCAATTTTCTCTTTACATTTAGCTGGTATTTCTTCTATTCTTGGAGCTATTAATTTTATCACAACAATTATTAATATGCGAATTAATAGTTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATCACAGCATTATTATTATTACTTTCTTTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATATCAACACTTATTT
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Type material. Holotype: ♂ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 64, bears the following five printed (text in italics handwritten) rectangular labels, four white: [TEXAS: | HIDALGO COUNTY | city of Mission | 10th Street at | irrigation ditch], [coll. | *29 OCT 1971* | Michael A. Rickard], [HESPERIIDAE, | Pyrginae: | Astraptes alector | hopfferi (Plotz, 1882) | det. R.O. Kendall | *♀(?)* M. & B. No. 37], [DNA sample ID: | NVG-14111E04 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | missionus Grishin]. The end of the abdomen of the holotype was probably lost early on, which resulted in Kendall's questionable determination of its sex (as labeled). The holotype appears to be a male, judging from its more elongated and pointed wings and the lack of white (or at least paler) scaling in the middle of the dorsal forewing characteristic of females in this species group.

Fig. 64. *Telegonus* (*Rhabdoides*) *missionus* **sp. n.** holotype ♂ NVG-14111E04 in dorsal (left) and ventral (right) views.

Type locality. USA: Texas, Hidalgo Co., Mission, 10th Street at irrigation ditch.

Etymology. The name is given for the type locality in Mission, Texas, and is treated as a masculine noun in apposition.

Distribution. Currently known only from the holotype collected in the lower Río Grande Valley of Texas, USA.

Suggested English name. Mission's Flasher.

Comment. The type locality of this species is also the type locality of *Spicauda atelis* Grishin, 2023, and it may have been around GPS 26.2168, −98.3311.

Telegonus (*Rhabdoides*) *panavenus* Grishin, new species

http://zoobank.org/FC50BC91-EE2B-40F6-886D-2322607EB90B

(Figs. 61 part, 63c–d, 65, 89 part)

Definition and diagnosis. Genomic analysis reveals that many specimens formerly identified as *Telegonus hopfferi* (Plötz, 1881) (type locality in Mexico, likely south-central or southern, lectotype sequenced as NVG-22068G07) are either *Telegonus gilberti* (H. Freeman, 1969) (type locality in Mexico, San Luis Potosí, holotype sequenced as NVG-15104B08) or closer related to *T. gilberti* than to *T. hopfferi* in the Z chromosome and the mitochondrial genome trees (Fig. 61b, c). Among them, three specimens from Panama and Venezuela are in the Z chromosome clade that is sister to *T. gilberti* (Fig. 61b) and are genetically differentiated from it at the species level: with F_{st}/G_{min}/COI barcode difference of 0.30/0.009/2.4% (16 bp). Therefore, they represent a new species. This species keys (incompletely) to "*Astraptes alector hopfferi*" C.14.26(a) in Evans (1952) but differs from it by having bluish rather than greenish overscaling at the wing bases and body above (similar to *T. gilberti*), the forewing beneath lacking traces of apical pale spots, paler overscaling along the costal margin and the discal cell pale spot are absent or vestigial; the blue area along the costal margin of the dorsal forewing extending distad to approximately the same level as in the discal cell, but extending farther along the inner margin, the forewing in males being uniformly brown distad of the blue third, without a paler area in the middle; and the ampulla being wider separated from the dorsal process of the harpe (Fig. 63d). Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly294.2.1:A591T, aly294.2.1:T1056C, aly294.2.1:A1086G, aly527.10.9:A55G, aly527.10.9:C117T; and COI barcode: T40C, A43T, T124C, A166G, T424T, T571C.

Barcode sequence of the holotype. Sample NVG-14111B08, GenBank PV550012, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATCGGTACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCTGGATCTTTAATTGGTGACGATCAAATTTATAATACT
ATCGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATGCCTATTATAATTGGAGGATTTGGAAATTGACTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCACCAAGGAGCATCAGTTGATTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAGATTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCTTTACCAGTTTTAGCAGGAGCTATCACTATATTATTAACTGATCGAAATCTAAATACCT
CATTTTTTGACCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Fig. 65. *Telegonus* (*Rhabdoides*) *panavenus* **sp. n.** holotype ♂ NVG-14111B08 in dorsal (left) and ventral (right) views.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 65, bears the following four printed (text in italics handwritten) rectangular labels, three white: [PANAMA:PANAMA | 5 mi N El Llano | 330m 9°17'N 79°00'W | *18.VI.1978* | leg. G.B.Small], [GENITALIA NO. | X-56 22 | J.M.Burns 2003], [DNA sample ID: | NVG-14111B08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | panavenus Grishin]. **Paratypes:** 2♂♂ in USNM: 1♂ NVG-14111B09 (leg DNA extraction, sequenced), NVG-23119E05 (abdomen DNA extraction and dissection) Panama, Veraguas Province, Ballena, 1-3-Feb-1979, G. B. Smal leg., genitalia NVG240817-44 (Fig. 63c–d) and 1♂ NVG-14111B12 Venezuela, Nueva Esparta, Isla de Margarita, La Sierra, 500 m, GPS 11.0167, −63.8833, 13-18-Mar-1988, R. K. Robbins leg.

Type locality. Panama: Panamá Province, 5 mi north of El Llano, elevation 330 m, approx. GPS 9.283, −79.000.

Etymology. The name is formed from the names of the counties with specimen records *Pana*[ma] + *Ven*[ezuela]+*us*. The name is treated as a masculine noun in apposition.

Distribution. Currently know from central Panama and Isla de Margarita in Venezuela.

Telegonus (*Rhabdoides*) *pacificus* Grishin, new species

http://zoobank.org/758A90B9-D934-4077-9A73-B04287A124AD

(Figs. 61 part, 63e–f, 66, 89 part)

Definition and diagnosis. Genomic analysis reveals that many specimens formerly identified as *Telegonus hopfferi* (Plötz, 1881) (type locality in Mexico, likely south-central or southern, lectotype sequenced as NVG-22068G07) are either *Telegonus gilberti* (H. Freeman, 1969) (type locality in Mexico, San Luis Potosí, holotype sequenced as NVG-15104B08) or closer related to *T. gilberti* than to *T. hopfferi* in the Z chromosome and the mitochondrial genome trees (Fig. 61b, c). Among them, two specimens from the western slopes on the Andes in Ecuador and Peru are in the Z chromosome clade that is sister to *T. gilberti* (Fig. 61b) and form a clade sister to the new species described in the previous section, being genetically differentiated from it at the species level with a COI barcode difference of 2.1% (14 bp). Therefore, they represent a new species. This species keys (incompletely) to "*Astraptes alector hopfferi*" C.14.26(a) in Evans (1952) but differs from it by having bluish rather than greenish overscaling at the wing bases and body above (similar to *T. gilberti*), the forewing beneath lacking traces of apical pale spots, pale overscaling along the costal margin being reduced, while the discal cell pale spot is well-developed, crossing the entire cell; the blue area along the costal margin of the dorsal forewing being the longest, and extending distad beyond blue areas in the discal cell, in males the forewing above being paler in the middle, giving an appearance of a pale area in the cell CuA_2-1A+2A that is heavily overscaled with brown; and the ampulla being closer associated with the dorsal process of the harpe and partly

Fig. 66. *Telegonus* (*Rhabdoides*) *pacificus* **sp. n.** holotype ♂ NVG-14111C02 in dorsal (left) and ventral (right) views.

overlapping it (Fig. 63e, f). Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly84.90.4:A223G, aly84.90.4:A399G, aly386.7.3:A570T, aly386.7.3:A645G, aly798.22.16:A15G; and COI barcode: T82C, T145T, A166A, A280G, T355C, T424T.

Barcode sequence of the holotype. Sample NVG-14111C02, GenBank PV550013, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCATTAAGATTACTTATTCGAACTGAATTAGGAACCCCTGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTCCCTCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTGACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTCTCATCCAATATTGC
CCACCAAGGAGCATCAGTTGACTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAGATTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCTTTACCAGTTTTAGCAGGAGCTATTACCATATTATTAACTGATCGAAATCTAAATACCT
CATTTTTTGACCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 66 (genitalia Fig. 63e, f), bears the following five printed rectangular labels, four white: [PERU: Piura: Rio | Pusmalca, 800m, | 05º23'S 79º37'W | & June 2000 | Robbins & Lamas Leg.], [DNA sample ID: | NVG-14111C02 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E06 | c/o Nick V. Grishin], [genitalia: | NVG240817-45 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | pacificus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratype:** 1♂ NVG-14111C01 Ecuador, Esmeraldas, km. 18.5 of San Mateo-Puerto Libre Rd., Zapallo hilltop, elevation 500 m, GPS 0.8853, −79.5450, 28-31-Aug-2002, J. P. W. Hall & M. A. Solis leg. [USNM].

Type locality. Peru: Piura Region, Río Pusmalca, elevation 800 m, approx. GPS −5.383, −79.617.

Etymology. The name is given for localities of the type series near the Pacific coast and is treated as a masculine noun in apposition.

Distribution. Currently known from near the Pacific coast and the western slopes of the Andes in Ecuador and Peru.

Investigations into *Papilio parmenides* Stoll, 1781

Papilio creteus Cramer, 1780 (type locality in Suriname) and *Papilio parmenides* Stoll, 1781 (type locality not stated in the description, likely in Suriname) have been treated as synonyms since Hübner ([1819]) and Herrich-Schäffer (1869), further supported by Godman and Salvin (1893) with the phrase: "There can be but little doubt that Cramer's *P. creteus* is the male of the species he subsequently described as *P. parmenides*, both types having been obtained in Surinam," and reaffirmed by Evans (1952). However, Steinhauser noticed several similar-looking species of *Telegonus* in the Guianas (unpublished, see below), as confirmed by our genomic analysis. Moreover, the original illustrations of these two species (Cramer 1780; Stoll 1781) differ from each other sufficiently to warrant additional investigation.

Published engravings may be rather inaccurate due to the reproduction process. Therefore, we consulted original drawings by Gerrit Wartenaar Lambertz in the library of BMNH, compiled and reproduced here in Fig. 67a, b. These originals show differences similar to those on published engravings. *Papilio creteus* has green wing bases and body, pale-yellow palpi beneath, and a paler ventral side of the wing with broader pale-brown bands and lacks a prominently paler streak near the hindwing tornus (Fig. 67a). *Papilio parmenides* has bluish green (greener on forewings) wing bases and body, pale bluish palpi beneath, a darker ventral side of wings with narrower paler bands, and a more prominent pale streak (posterior part of the outer paler band) by the hindwing tornus (Fig. 67a). Due to rounder hindwing tornus, this illustrated specimen (or specimens, it is possible that the dorsal and ventral drawings show different specimens) might have been a female (or females), but not necessarily, because the positioning of wings and possible wing damage (e.g., as in Fig. 67c) might have caused an artifact in the illustration drawn from a male.

We searched for primary type specimens of these taxa. Two males of similarly spread *Telegonus* were found in RMNH, originally from the Calkoen collection. One of them is illustrated in Fig. 67c.

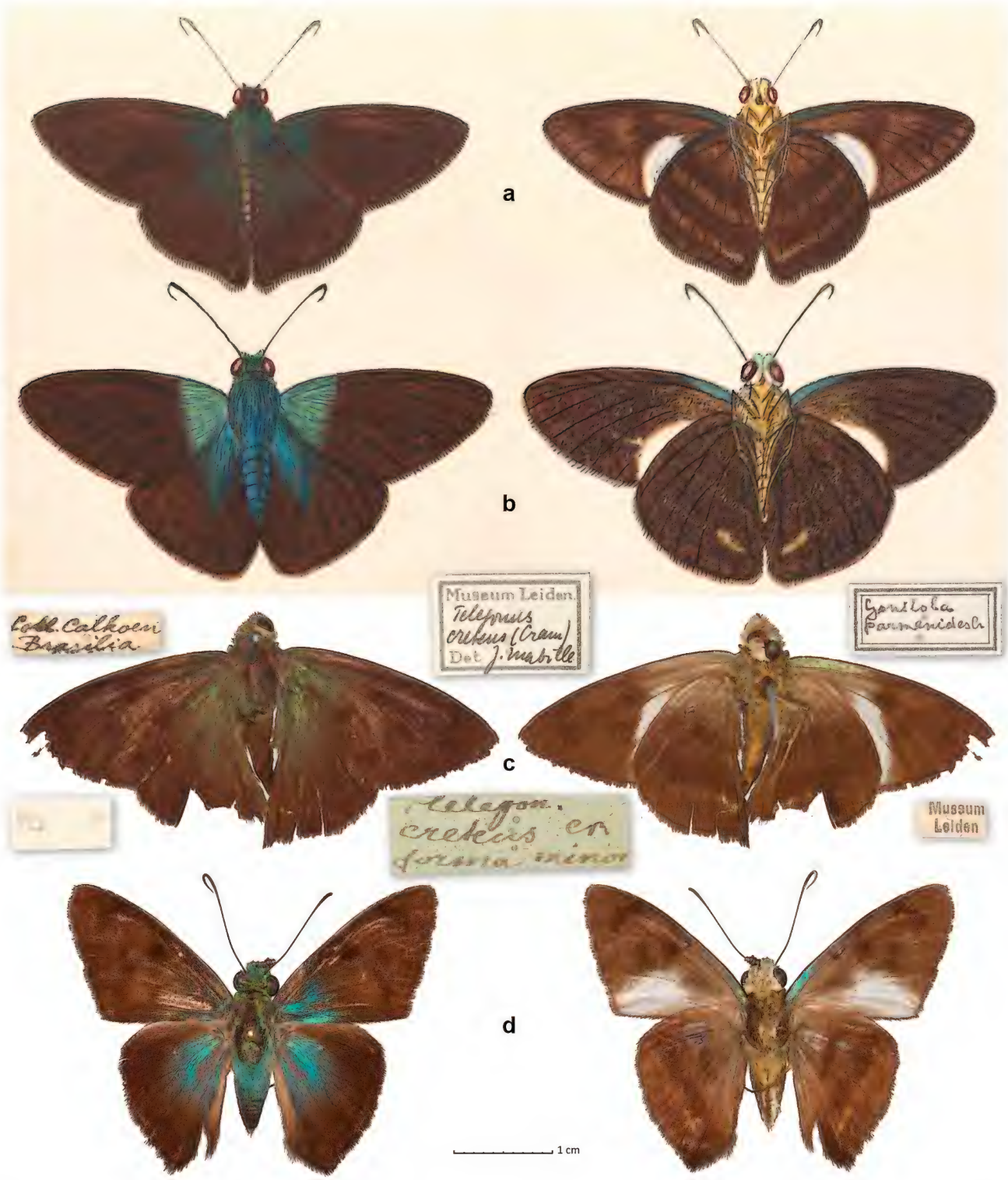


Fig. 67. *Telegonus creteus* and *Telegonus parmenides* **stat. rest.** in dorsal (left) and ventral (right) views: original drawings by Lambertz of type specimens of: **a)** *Papilio creteus* and **b)** *Papilio parmenides* used as models for published engravings; **c)** a male from Brazil in the Calkoen collection (known to include Cramer's primary types) with its original labels [RMNH]. This specimen resembles the drawing of *Papilio parmenides* and is conspecific with the specimen from Guyana in MGCL that was chosen by Steinhauser as the neotype of *P. parmenides*, although this designation remains unpublished; **d)** a male we identify as conspecific with the Calkoen specimen shown in **c)**, from Suriname, savanna forest adjacent to airport, Mar-2002, M. J. Simon leg., NVG-22078G06 [MGCL]. Images shown in **a)** and **b)** are © The Trustees of the Natural History Museum London and are made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/).

Fig. 68. Male genitalia of *Telegonus* (*Rhabdoides*) non-type specimens [MGCL]: **a–j)** *T. creteus*: **a–e)** NVG-22078G05 Venezuela, Amazonas, Samariapo, Upper Orinoco, upstream from Maipures Rapids, 95–115 m, 5-Sep-1946, Rene Lichy leg., vial SRS-1799 and **f–j)** NVG-22078G04 Brazil, Pará, Fazenda Velna nr. Belém, 17-Nov-1973, C. Callaghan leg., vial SRS-853 and **k–s)** *T. parmenides*: **k–p)** NVG-24064B01 French Guiana, Maroni River, Oct-Nov-1903, ex coll. Le Moult, vial SRS-1786 and **q–s)** NVG-23063F08 Brazil, Amazonas, Manaus, km 26 AM-010, Reserva Ducke, GPS −2.9167, −59.9833, 13-Dec-1993, J. Bolling Sullivan & Roger W. Hutchings leg., vial SRS-4607 in different views: **a**, **c–f**, **h–k**, **n–p**, **r)** left lateral; **b**, **g**, **l**, **s)** dorsal; **q)** right lateral; and **m)** ventral: **q–s)** complete genital capsule and **a**, **b**, **f**, **g**, **k–m)** genitalia with **c**, **h**, **n)** aedeagus and **d**, **i**, **o)** right and **e**, **j**, **p)** left valvae detached and shown separately. Vesica is everted in **c)**, cornuti pointing up at uncus in **a)**. Beige arrows connect different views or parts of the same genitalia.

Among the Calkoen material are a number of Cramer primary type specimens (de Jong 1983). However, these two specimens are labeled from "Brasilia" (and not from Suriname as per the description of *P. creteus*) and differ in several details from the illustrated specimens. While the Lambertz's drawings are not expected to be particularly accurate, the Calkoen specimens are not as pale beneath as the illustrated *P. creteus* and their palpi are not pale bluish as in *P. parmenides*, also mentioned in its original description as (translated): "The green and blue coloration on both sides of head" (Stoll 1781). However, the Calkoen specimens were collected at approximately the same time as the types, and they are spread

similarly. Being darker beneath with narrower paler bands and better developed pale streak by the ventral hindwing tornus, they are more similar to the drawings of *P. parmenides* than *P. creteus*. Because the locality of *P. parmenides* was not mentioned in the original description, it is even possible that the Calkoen specimens from Brazil might have been syntypes of *P. parmenides*, if there were several syntypes, but probably not the syntype(s) illustrated by Lambertz.

Further analysis reveals that these two Calkoen specimens are conspecific with the specimen from Guyana (NVG-15039E06) in MGCL selected by Steinhauser as a candidate neotype of *P. parmenides* that remained unpublished. Moreover, this species is present in Suriname, as evidenced by a more recently collected specimen NVG-22078G06 (MGCL) shown in Fig. 67d. We do disagree that the specimen selected by Steinhauser is the best candidate for the neotype of *P. parmenides*, mainly because it is from Guyana and not from Suriname, and it differs from the original drawing in the following characters: bluish-green overscaling on both wings is about the same color in the specimen, while the drawing shows distinctly greener forewings and bluer hindwing (coloration we observed in some specimens of *Telegonus*); its palpi are not as green beneath as in the drawing (although with green scales); and the pale streak near the tornus of the ventral hindwing is not as pronounced as in the drawing.

Nevertheless, the evidence assembled above argues that Calkoen specimens from Brazil, the candidate neotype by Steinhauser from Guyana, and a male from Suriname may indeed represent the original *P. parmenides*. Therefore, we presently apply the name *Papilio parmenides* Stoll, 1781 to the species represented by NVG-15039E06 and NVG-22078G06 (Fig. 67d) and are searching for a specimen (not necessarily of the same species) that agrees best with all available information about this taxon to be designated as its neotype. Male genitalia of this species are shown in Fig. 68k–s and are characterized by a concave costa of the valva and a distally pointed, but not strongly elongated harpe with a relatively straight dorsodistal margin that is not concave but with a vestigial hump in the middle.

Lectotype designation for *Telegonus bifascia* (Herrich-Schäffer, 1869) confirming it and *Telegonus tinda* (Evans, 1952) as species distinct from *Telegonus latimargo* (Herrich-Schäffer, 1869)

Evans (1952) treated *Eudamus bifascia* Herrich-Schäffer, 1869 (type locality in tropical America to USA, likely in Brazil, as evidenced by genomic sequencing, syntype sequenced as NVG-15031C04) and *Astraptes latimargo tinda* Evans, 1952 (type locality in Brazil: Pará) as subspecies of *Telegonus latimargo* (Herrich-Schäffer, 1869) (type locality in tropical America to USA, lectotype sequenced as NVG-15031C08), but he misidentified both *E. bifascia* and *T. latimargo*. According to the genomic analysis (Fig. 61) and phenotypic inspection of the *E. bifascia* syntype, it is a species closely related to *Telegonus siges* Mabille, 1903 (type locality in Brazil, specimens known from South Brazil), with the latter taxon placed as a subspecies of the former in the next section. Specimens that Evans misidentified as "*Astraptes latimargo bifascia*" belong to several undescribed species, some of which are discussed below.

The syntype of *E. bifascia* we sequenced is labeled as a type specimen of this taxon, is from the Herrich-Schäffer collection according to its labels, and matches the original description, parts of which we assemble from the identification keys and translate as: "Underside with a faintly paler outer-marginal quarter to [outer-marginal] sixth [of the wing's width]. Fringes brown, underside with two broad darker irregular transverse bands through all wings." Therefore, we agree that this specimen is a syntype. To stabilize nomenclature and define the name *E. bifascia* objectively, N.V.G. hereby designates this syntype in the MFNB collection with the following eleven rectangular labels (1st purple, 9th yellow, others white): [Origin.], [Eudamus bifascia HS | N. W. 16 Bras. Pr. 24], [Coll. H.–Sch.], [Teleg. Bifascia | HS.], [Bifascia H-Sch.], [14:23.], [Allyn Museum Photo | No. 830113/7,8, | 9,13,14], [Genit. Prep. | SRS-1077], [Zool. Mus. | Berlin], [{QR Code} http://coll.mfn-berlin.de/u/ | 940b09], and [DNA sample ID: | NVG-15031C04 | c/o Nick V. Grishin] as the **lectotype** of *Eudamus bifascia* Herrich-Schäffer, 1869. The lectotype has a chipped outer margin of the left forewing at about its middle and a deep tear

stemming from it. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15031C04, GenBank PV550014, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGTACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCTGGATCTTTAATTGGTGATGATCAAATTTACAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCACCAAGGAGCATCAGTTGACTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCCTCTATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAGATTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCTTTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATCTAAATACCT
CATTTTTTGACCCCGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Genomic sequencing agrees with the label stating "Bras[il]." and places the lectotype with the specimens from Brazil, which is a likely type locality that we should be able to narrow down further by sequencing additional specimens. The label [14:23.] corresponds to the number for *Telegonus cretellus* (Herrich-Schäffer, 1869) (type locality in Jamaica as deduced by genomic sequencing and phenotypic comparison (Zhang et al. 2022b)) in Mabille's catalog, where the locality for *T. cretellus* is given as "Brésil" (Mabille 1903). This label was not photographed by Hermier before our analysis, and it was not on the *T. cretellus* lectotype either at that time. This label might have fallen off another *cretellus*-like specimen and been placed on the *E. bifascia* lectotype by mistake.

According to the genomic analysis (Fig. 61) and phenotypic inspection of the *Eudamus latimargo* lectotype (see below) and comparing it with the specimens that Evans identified as such, Evans's "*Astraptes latimargo latimargo*" is not this species but is conspecific with the lectotype of *Thymele grullus* Mabille, 1888 (type locality in Panama: Chiriquí, sequenced as NVG-15031B12), a species-level taxon and not, as currently considered, a synonym of *Telegonus latimargo* (see below). Thus, inspecting the genomic trees, we see that *Telegonus bifascia* (Herrich-Schäffer, 1869), **stat. conf.**, *Telegonus tinda* (Evans, 1952), **stat. conf.**, and *Telegonus latimargo* (Herrich-Schäffer, 1869) belong to three different species groups (Figs. 61, 89) and are valid species that are strongly different from each other genetically.

Telegonus parmenides (Stoll, 1781), *Telegonus bifascia siges* Mabille, 1903, *Telegonus crana* (Evans, 1952), *Telegonus cyprus* (Evans, 1952), and *Telegonus cyprus crilla* (Evans, 1952) are taxa distinct from *Telegonus creteus* (Cramer, 1780)

Similarly to *Papilio parmenides* Stoll, 1781 (type locality not stated in the original description, likely in Suriname) analyzed above, falling short of the neotype designation for *Papilio creteus* Cramer, 1780 (type locality in Suriname) and pending further studies, we tentatively identify *P. creteus* consistently with Steinhauser (unpublished, specimens identified by Steinhauser as *P. creteus* sequenced from several collections). Male genitalia of this species are shown in Fig. 68a–j and are characterized by a straight or bisinuate costa of the valva formed by an expanded anteriad and stronger sclerotized ampulla, and a distally more rounded and not strongly elongated harpe with a relatively straight dorsodistal margin without a hump in the middle. This is the species Evans (1952) misidentified as "*Astraptes chiriquensis oenander*" (in part, see below).

Assuming that our identification of *P. creteus* is correct, genomic analysis reveals that *P. parmenides* and the following taxa treated by Evans (1952) as subspecies of "*Astraptes creteus*", currently in the genus *Telegonus* Hübner, [1819] (type species *Papilio talus* Cramer, 1777), i.e., *Telegonus siges* Mabille, 1903 (type locality in Brazil), *Astraptes creteus crana* Evans, 1952 (type locality Guatemala: San Gerónimo), and *Astraptes creteus cyprus* Evans, 1952 (type locality in Bolivia) are genetically differentiated from each other at the species level and are placed in different clades of the phylogenetic trees (Fig. 61). They are also distinct from other taxa, and among them, only *T. siges* is rather closely related to another named species, *Telegonus bifascia* (Herrich-Schäffer, 1869) (type locality in Tropical America to USA, likely Southeast Brazil as evidenced by our genomic sequencing) (Fig. 61) that Evans (1952) misidentified (see previous section): COI barcode difference of 0.8% (5 bp). *Telegonus bifascia* and *T. siges* do not separate into distinct clades in our nuclear genome trees, do not strongly differ genetically with F_{st}/G_{min} of 0.06/0.05, and, pending further studies, the latter taxon may be regarded as a subspecies of the former due to some genetic differentiation between them (Fig. 61). Therefore, we

propose to treat *Telegonus parmenides* (Stoll, 1781), **stat. rest.**, *Telegonus bifascia siges* Mabille, 1903, **comb. nov.**, *Telegonus crana* (Evans, 1952), **stat. nov.**, and *Telegonus cyprus* (Evans, 1952), **stat. nov.** as taxa distinct from *Telegonus creteus* (Cramer, 1780).

We also find that *Astraptes creteus crilla* Evans, 1952 (type locality Ecuador: Zamora) is in a different clade from *Telegonus creteus* (Cramer, 1780) and instead is closely related to *Telegonus cyprus* (Evans, 1952), **stat. nov.** (Fig. 61). The two names *A. creteus cyprus* and *A. creteus crilla* were proposed at the same rank in the same work issued on the same date (Evans 1952). As the first reviser, we gave precedence to *A. creteus cyprus* above, and, therefore, conservatively place *A. creteus crilla* as its subspecies, *Telegonus cyprus crilla* (Evans, 1952), **comb. nov.**, pending further studies of additional specimens. Male genitalia of the *T. cyprus crilla* specimen we sequenced are shown in Fig. 63k, l, and are typical for the group in having a concave costa of the valva, a dorsally protruding ampulla separated from the dorsal process of the harpe by a narrow gap, and a distally pointed harpe with a concave dorsoposterior margin.

Investigations into *Eudamus oenander* Hewitson, 1876

Eudamus oenander was described by Hewitson (1876) from an unstated number of specimens from Pará, Brazil, in the Staudinger collection. The description is short, and its major part, written in English that expands on the Latin preamble, is quoted here in its entirety: "Upperside rufous-brown, the base of both wings blue. Underside rufous-brown. Anterior wing with the costal margin blue from the base to the middle, the inner margin broadly white. Posterior wing lobed, darker at the middle, followed by a band of paler colour. Exp. 1 6/10 inch. Hab. Pará. In the collection of Dr. Staudinger." This description likely refers to a single specimen, because no others were mentioned, and a single measure (not a range) is given for wingspan. Nevertheless, avoiding the assumption of the holotype to follow the ICZN Code Recommendation 73F (ICZN 1999), we consider any type specimens of *E. oenander* to be syntypes.

No known *E. oenander* syntypes have been reported (Evans 1952; Steinhauser 1987). If they are still extant, they could be in MFNB (most likely) and possibly in ZSMC, or even MTD (the least likely possibility), where the specimens from the Staudinger collection are currently housed. N.V.G. searched for the syntypes of *E. oenander* in Hesperiidae holdings of these three collections, including unsorted material. Known Hewitson syntypes in the Staudinger collection bear a label with a single word in Hewitson's handwriting: the taxon name. For instance, a male syntype of *Eudamus aegiochus* Hewitson, 1876 (currently in the genus *Celaenorrhinus* Hübner, [1819]), described in the same publication with *E. oenander*, is housed in the MFNB collection, and bears such a label "*Ægiochus*". Syntypes of *E. oenander* were not found, and we proceeded to figure out the taxonomic identity of *E. oenander* from its description and other publications.

Williams and Bell (1934) synonymized *E. oenander* with *Telegonus creteus* (Cramer, 1780) (type locality in Suriname): "The description of *oenander* indicates a typical *creteus*, of which, Capt. Riley informs us, there is no specimen in the Hewitson Collection, nor is there any specimen under the name *oenander*." Evans (1952) treated *E. oenander* as "*Astraptes chiriquensis oenander*", also placing it with species currently in the genus *Telegonus* Hübner, [1819] (type species *Papilio talus* Cramer, 1777). However, according to the original description, *E. oenander* is a medium-sized species, about 4 cm in wingspan (1 6/10 inches). Even if it is spread with forewings pulled up to minimize the wingspan, specimens of *Telegonus* are rarely this small (e.g., some *T. parmenides*). Furthermore, the description does not match *Telegonus* in its details, e.g., we are yet to find a *Telegonus* specimen with the blue along the forewing costa beneath reaching its middle, rarely its third, and the ventral hindwing is typically with two variously developed bands, not "darker in the middle" with the paler band distad of the darker area.

Therefore, judging from the specimen size, blue wing bases above, forewing beneath with blue costa to its middle and large white tornal area, and lobed hindwing beneath with central dark area with a paler band distad, *E. oenander* could have been a species of *Ectomis* Mabille, 1878, *Aroma* Evans, 1955, or possibly some other medium-sized species in this mimicry complex. Several known *Ectomis* species (e.g., *Ectomis bahiana* (Herrich-Schäffer, 1869) and males of *Ectomis pervivax* (Hübner, [1819])) agree

with Hewitson's description, but they also have bluish ventral hindwing bases, and at least a trace of a white spot in the middle of the ventral forewing costal margin. These two obvious characters were not mentioned in the original description, and therefore, it is less likely that *E. oenander* belongs to *Ectomis*. Conversely, *Aroma aroma* (Hewitson, 1867) (type locality in Brazil: Pará) agrees with the description nearly perfectly, and *Eudamus oenander* may be this species, re-described by Hewitson from the same locality nearly a decade later. Moreover, another species of *Aroma* was proposed by Staudinger (1875) in the genus *Telegonus* as *T. henricus*, highlighting similarities in appearance between these species as a source of confusion about their classification. Therefore, we propose to treat *Eudamus oenander* Hewitson, 1876 as a junior subjective synonym of *Aroma aroma* (Hewitson, 1867), **new synonym placement**, while we continue our search for syntypes of this taxon.

We conclude that *E. oenander* does not belong to *Telegonus*, and Evans (1952) misidentified this species. We employ the name *Telegonus creteus* (Cramer, 1780) (type locality in Suriname) for some specimens that Evans (1952) identified as "*Astraptes chiriquensis oenander*" because out of all *Telegonus* species currently known from the Guianas, these specimens match best the original description and illustrations of *T. creteus*. Furthermore, the name of the species Evans (1952) identified as "*Astraptes creteus creteus*" is *Telegonus parmenides* (Stoll, 1781) (type locality in Suriname), according to our investigation presented above. Evans (1952) treated *T. parmenides* as a junior subjective synonym of his "*A. creteus creteus*".

Telegonus (*Rhabdoides*) *amazonicus* Grishin, new species

http://zoobank.org/28F5F9C3-EC96-4B44-A158-0C912E4B556A

(Figs. 61 part, 63g–h, 69, 89 part)

Definition and diagnosis. Genomic analysis reveals that many specimens formerly identified as *Telegonus hopfferi* (Plötz, 1881) (type locality in Mexico, likely south-central or southern, lectotype sequenced as NVG-22068G07) are either *Telegonus gilberti* (H. Freeman, 1969) (type locality in Mexico, San Luis Potosí, holotype sequenced as NVG-15104B08) or closer related to *T. gilberti* than to *T. hopfferi* in the Z chromosome and the mitochondrial genome trees (Fig. 61b, c). Among them, several specimens from the Amazonian region are not in the same clade as *T. gilberti* but are sister to the clade consisting of *Telegonus bifascia bifascia* (Herrich-Schäffer, 1869) (type locality in tropical America to USA, likely in Brazil, as evidenced by genomic sequencing of the lectotype NVG-15031C04) and *Telegonus bifascia siges* Mabille, 1903, **comb. nov.** (type locality in Brazil) in the nuclear genome (Fig. 61a, b) being genetically differentiated from them at the species level and not monophyletic with them in the mitochondrial genome tree (Fig. 61c) with a COI barcode difference of 1.1% (7 bp). Therefore, they represent a new species. Curiously, *T. bifascia*, the closest relative according to the nuclear genome (Fig. 61a, b), lacks the white area along the costal margin at the base of the ventral hindwing characteristic of the new species. This species keys to "*Astraptes alector hopfferi*" C.14.26(a) in Evans (1952) and while having greener rather than bluer overscaling at the wing bases and body above, is darker beneath with the white overscaling much restricted or absent along the forewing costal margin, the central white band is more like a tornal spot, typically not entering the discal cell in males (one paratype has a small whitish cell spot near its posterior end), the greenish area extends farther distad in the discal cell and along the inner margin than along the costal margin, while bluish extends the longest along the costal margin in *T. panavenus* **sp. n.** (see above) and about the same level as in the discal cell in other close relatives; no traces of subapical forewing pale spots beneath (or above), but some males have a diffuse paler spot in the middle of the dorsal forewing; females are with such a spot, which may be paler and larger, trapezoidal in the cell CuA_1-CuA_2 with traces of paler areas in the discal cell and the cell CuA_2-1A+2A, and the forewing beneath is with a white spot in the posterior half of the discal cell. The ampulla is narrower and closer associated with the dorsal process of harpe; this process is more robust (Fig. 63h). Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly3319.1.3:C45T, aly3762.23.7:G168A, aly3762.23.7:T150C, aly15386.1.1:C516A, aly15386.1.1:T531A; and COI barcode: T49A, T145C, C349C, T355T, T361T, T424T.

Barcode sequence of the holotype. Sample NVG-14111C03, GenBank PV550015, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCATTAAGATTACTTATTCGAACTGAATTAGGAACTCCTGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATCATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTCTCATCTAATATTGC
CCACCAAGGAGCATCAGTTGACTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAGATTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCTTTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATCTAAATACCT
CATTTTTTGACCCCGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 69 (genitalia Fig. 63g, h), bears the following six rectangular labels (2nd handwritten and others printed), five white: [BRASIL: Rondonia | 62km S Ariquemes | Faz.Rancho Grande 165m | 10°53'S, 62°80'W. 19-29. | Sept.1996. B.Harris], [Astraptes | alector], [DNA sample ID: | NVG-14111C03 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E07 | c/o Nick V. Grishin], [genitalia: | NVG240817-46 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | amazonicus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratypes:** 10♂♂ and 5♀♀: Brazil, Rondônia, 62 km S of Ariquemes, linha C-20, Fazenda Rancho Grande, G. T. Austin leg. [MGCL]: 1♂ NVG-24073H10 linha C-20, 10 km E of B-65, 3 km E of, 18-Nov-1992 and 1♂ NVG-24073H11 7 km E of B-65, 14-Nov-1992; 1♀ NVG-24033H09 Pará, 1896, Donckier leg. [MFNB]; and Amazonas: 1♂ NVG-24073H09 Maués, Rio Apoquitaua, Feb-1999, M. Simon leg. [MGCL]; 1♂ NVG-24034B05 Massauari, old, Hahnel leg. [MFNB]; and 1♂ NVG-24034B03 Tefé, old, Hahnel leg. [MFNB]; 1♀ NVG-21115D05 Suriname, Berg en Dal, 1873, L. leg. (we were not able to deduce the name behind the abbreviation "L.") [MFNB]; 1♀ NVG-14111B11, USNMENT 00275055 Guyana, Eastern Kanuku Mountains, Two Hat Mountain south slope, elevation 850'–1200', GPS 3.1133, −59.0983, 21-28-Sep-2000, S. Fratello et al. leg. [USNM]; 1♀ NVG-24073G02 Venezuela, Amazonas, Puerto Ayacucho, 29-Aug-1999, M. Simon leg. [MGCL]; 1♂ NVG-14111B10 Colombia, Caquetá Department, La Montañita, elevation 350 m, 27-Jan-1971, S. S. & S. Nicolay leg. [USNM]; Ecuador: 1♂ NVG-19071H06, USNMENT 01588529 Napo Province, Misahualli Jungle Lodge, elevation 450 m, GPS −1.0257, −77.6570, 6-8-Jan-2002, J. P. W. Hall & M. A. Solis leg. [USNM] and 1♀ NVG-24034B06 Pastaza Province, Sarayacu, old [MFNB]; Peru: 1♂ NVG-19071H07, USNMENT 01588530 Loreto Region, 25 mi E of Iquitos, Amazon River, Explorama Inn, elevation 200 m, 17-21-Sep-1990, Ron Leuschner leg. [USNM] and 1♂ NVG-24074A02, Huánuco, Tingo María, ca. 2007, E. C. Knudson leg. [MGCL]; and 1♂ NVG-24034B04 Bolivia, Beni, Puerto San Mateo, 1891, Garlepp leg. [MFNB].

Type locality. Brazil: Rondônia, 62 km south of Ariquemes, linha C-20, 7 km east of B-65, Fazenda Rancho Grande, elevation 165 m, approx. GPS −10.53, −62.80.

Etymology. The name is derived from the distribution of this species confined to the Amazonian Region. The name is treated as a masculine noun in apposition.

Distribution. The Amazonian Region, broadly in all countries.

Fig. 69. *Telegonus* (*Rhabdoides*) *amazonicus* **sp. n.** holotype ♂ NVG-14111C03 in dorsal (left) and ventral (right) views.

Telegonus (*Rhabdoides*) *pallidus* Grishin, new species

http://zoobank.org/F10DDFE4-038B-40DF-94D0-FE6F2DAE6772

(Figs. 61 part, 63i–j, 70, 89 part)

Definition and diagnosis. A sequenced specimen from Panama (in USNM collection) that is phenotypically similar to Ecuadorian *Telegonus cyprus crilla* (Evans, 1952), **comb. nov.** due to the presence of a pale spot in the middle of the dorsal forewing is not monophyletic with it in trees constructed from the autosomes in the nuclear genome (Fig. 61a) and the mitochondrial genome (Fig. 61c), and instead is closer related to *Telegonus crana* (Evans, 1952), **stat. nov.** (type locality Guatemala: Geronimo), being genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcode difference is 3.5% (23 bp). Therefore, this Panamanian specimen represents a new species. This new species keys to "*Astraptes creteus crilla*" C.14.28(b) in Evans (1952) due to the presence of a white spot in the middle of the dorsal forewing, but differs from it by this spot being smaller and stronger overscaled with brown around its edges, the pale area in the ventral forewing discal cell being heavier overscaled with brown, especially along the vein, and a more elongated hindwing. The new species differs from *T. crana*, to which it is closely related, by being paler, as reflected in having a pale spot and a smear around it in the middle of dorsal forewing; a paler costal area from the base to the middle of the ventral forewing (browner in *T. crana*), this area is also merged with the central band; and heavier yellowish overscaling on the ventral hindwing. The ampulla is smaller and wider separated from the dorsal process of the harpe (Fig. 63i). Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1651.38.1:T651C, aly1651.38.1:C1146T, aly839.26.4:G214A, aly839.26.4:A224T, aly536.8.1:G510A, aly276890.2.8:A45A (not G), aly276890.2.8:C63C (not T), aly322.44.3:T42T (not C), aly322.44.3:T52T (not G), aly222.2.10: G90G (not T); and COI barcode: A100C, C220T, T292C, T232C, C364C, T400C, C478C.

Barcode sequence of the holotype. Sample NVG-14111D04, GenBank PV550016, 658 base pairs:

AACTTTATACTTTATTTTTGGAATTTGAGCAGGATTAGTTGGAACCTCTTTAAGTTTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGCGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCTTTAATAATAGGAGCTCCTGATATAGCCTTTCCACGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATCTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAACATCAGTTGACTTAGCAATTTTTTCCCTACACTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAACTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTTGGAATTACAGCATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAACTTAAATACTT
CATTTTTTGACCCAGCGGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 70 (genitalia Fig. 63i, j), bears the following five printed rectangular labels, four white: [PANAMA: Darien | Cana 1550m | 5.VI.1983 | Leg. G. B. Small], [DNA sample ID: | NVG-14111D04 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E08 | c/o Nick V. Grishin], [genitalia: | NVG240817-47 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | pallidus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Fig. 70. *Telegonus* (*Rhabdoides*) *pallidus* **sp. n.** holotype ♂ NVG-14111D04 in dorsal (left) and ventral (right) views.

Type locality. Panama: Darién Province, Cana, elevation 1550 m.

Etymology. The name is given for the paler aspect of this species compared to its relatives. The name is a masculine adjective.

Distribution. Currently known only from the holotype collected in eastern Panama.

Telegonus (*Rhabdoides*) *subfuscus* Grishin, new species

http://zoobank.org/11069080-89AE-4111-8603-86E70A3E775B

(Figs. 61 part, 63m–o, 71, 89 part)

Definition and diagnosis. A male from Santa Catarina, Brazil (in MGCL collection) identified as "*T. bifascia*" is not even in the same species group with *Telegonus bifascia* (Herrich-Schäffer, 1869) (type locality in tropical America to USA, likely in Brazil, as evidenced by genomic sequencing, lectotype sequenced as NVG-15031C04) but instead is closer related to the phenotypically different *Telegonus cyprus* (Evans, 1952), **stat. nov.** (type locality in Bolivia) while being genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 4.3% (28 bp). Therefore, this misidentified "*T. bifascia*" represents a new species. This new species keys (incompletely) to "*Astraptes creteus siges*" C.14.28(e) in Evans (1952) but differs from it (and the very similar *T. bifascia*) by the ventral forewing postdiscal band in males being in the middle between discal and apical bands, aquamarine-colored wing bases and body above (not blue or greenish-yellow), darker forewing apex beneath continuing as an outer-marginal darker band, and narrower ventral hindwing dark bands in males. It differs from its sister species *T. cyprus* by having a much darker appearance beneath, e.g., a reduced pale area by the forewing tornus and the lack of a pale cross-band; more prominent dark spots nearly connected into bands, and a narrower hindwing. The valva is narrower in the middle as a result of a more concave costa and more constricted valva at its transition to the harpe; the ampulla is smaller, nearly triangular in lateral view, and wider separated from the dorsal process of the harpe (by a U-shaped groove); this process is narrower and longer; the harpe is terminally extended and its dorsoposterior margin is with a broad and shallow hump in the middle (Fig. 63m, o). Due to the cryptic nature of this species (compared to *T. bifascia*), most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly537.19.6:C123T, aly275211.5.10:A624G, aly275211.5.10:G630T, aly1019.10.2:A1041G, aly235.14.1:G1496A; and COI barcode: A28G, T70C, T187C, T382C, T589C, T652C.

Barcode sequence of the holotype. Sample NVG-22078G12, GenBank PV550017, 658 base pairs:

AACTTTATACTTTATTTTTGGAATTTGGGCAGGATTAGTTGGAACCTCTTTAAGTTTACTTATTCGAACCGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGATTAGTCCCCTTAATAATAGGAGCCCCTGATATAGCTTTCCCACGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
TCATCAAGGAGCATCAGTCGACTTAGCAATTTTTTCTTTACACTTAGCTGGTATTTCTTCCATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTATTTGAGCTGTTGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGACCGAAACTTAAATACTT
CATTTTTTGATCCAGCAGGAGGAGGAGATCCAATTTTATACCAACACTTATTT

Fig. 71. *Telegonus* (*Rhabdoides*) *subfuscus* **sp. n.** holotype ♂ NVG-22078G12 in dorsal (left) and ventral (right) views.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 71 (genitalia Fig. 63m–o), bears the following six printed (text in italics handwritten) rectangular labels, five white: [Brazil,S.Catarina | Joinville 200m. | March 13-14, 1984 | McInnis, Coll.], [Genit. Vial | SRS-*3219*], [*Telemachus bifascia* | *(Herrich-Schäffer, 1869)* | ♂ | Det. S. R. Steinhauser], [CV Covell colln. | MGCL Acc. | 2006-9], [DNA sample ID: | NVG-22078G12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | subfuscus Grishin]. **Paratype:** 1♀ NVG-23063F09 Brazil, Espirito Santo, Santa Teresa, elevation 800 m, 13-15-Feb-1972, C. Callaghan leg., genitalia vial SRS-1801 [MGCL].

Type locality. Brazil: Santa Catarina, Joinville, elevation 200 m.

Etymology. The name is given for the ventral side (*sub-*) being darker (*fuscus*) than in its relatives. The name is a masculine adjective.

Distribution. South Brazil.

Comment. We list data on all labels of the holotype, verbatim, including identification labels. One of such labels contains an unpublished name "Telemachus." Here, we use Art. 8.3. of the ICZN Code and disclaim the name "Telemachus" for nomenclatural purposes. Thus, we consider this name to be unpublished.

Neotype designation for *Eudamus blasius* Plötz, 1881

The name *Eudamus blasius* Plötz, 1881 (type locality listed as "Cuba", likely in Southeast or South Brazil) was proposed to include specimens that Herrich-Schäffer (1869) had identified as *Goniloba elorus* (Hewitson, 1867), but which Plötz (1881) suggested were misidentified. However, Godman (1907) who inspected the unpublished and now likely lost original drawing by Plötz of *E. blasius* syntype (taf[el]. 93), decided that it was conspecific with *Telegonus* (*Rhabdoides*) *elorus* (Hewitson, 1867) (type locality in Brazil, likely Southeast or South). Since then, the name *blasius* has been treated as a junior subjective synonym of *T. elorus* in most publications (Evans 1952; Mielke 2005). Skinner and Ramsden (1923) doubted the type locality "Cuba" given by Plötz for *E. blasius* because no specimens matching the original description were known from Cuba. Specimens agreeing with the description are only known from Southeast and South Brazil.

To learn more about *E. blasius*, we interpretively translate its original description, assembling relevant sections of the key given by Plötz (1881): "the body and wing bases are blue or green above; forewing beneath lacks a white spot near mid-costa and is brown [not blue] at the base; ventral side of all wings is light brown along the margin and sharply bordered by a dark brown postdiscal band; tornus of the hindwing beneath is shaded dull brown up to vein 2 [i.e., CuA_2]." We regard these as characters to differentiate *E. blasius* from other taxa.

To gain further insights, we searched for *E. blasius* syntypes among Hesperiidae holdings in all major collections that are listed in the Acknowledgments section. We focused on the MFNB collection, which contains many primary types of Plötz and Herrich-Schäffer. Several specimens in MFNB bear the identification label "blasius" but none has a label characteristic of specimens from the Herrich-Schäffer collection and can be directly linked with it. One of these specimens is also labeled as "Typus." However, according to its labels, this specimen from the Weymer collection was collected in 1894, which is after the original description of *E. blasius*, and, therefore, is not a syntype. This is most likely a specimen of *Telegonus blasius* mentioned by Weymer (1895), according to whom, it was from Rio Grande do Sul in Brazil. This specimen mostly agrees with the original description of *E. blasius*, particularly in exhibiting a strong contrast between the paler wing margins beneath and a postdiscal dark band, but it does not have a prominently darker ventral hindwing tornus up to vein CuA_2. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024).

The second specimen (Fig. 72b) labeled as "blasius" is also from the Weymer collection and agrees less with the original description due to weaker contrast between the submarginal pale and

postdiscal brown, but it has a darker tornus. The third specimen (Fig. 72a) bears a label characteristic of many Plötz's type specimens, penciled on a yellowing paper "blasius Pl. (elorus H-Sch nec Hew.)" and agrees best with the original description of *E. blasius* both in having a strong contrast between pale margins and dark bands on both wings beneath and a darker tornus bordered precisely by the vein CuA_2 on the ventral hindwing. This is an old specimen with "repair" characteristic of century-old specimens when pieces of wings of some other specimens were glued on to cover missing parts of wings: both wings are repaired at the tornus from beneath. However, this specimen lacks any labels linking it to Herrich-Schäffer or Plötz directly. Judging from its age, agreement with the original description of *E. blasius*, and its identification label, it is possible that this specimen is a syntype of *E. blasius*. However, we do not have strong evidence to support this hypothesis. Therefore, we consider that syntypes of *E. blasius* are either lost or are unrecognizable.

Genomic sequencing reveals that at least two similar-looking species have been identified as *T. elorus*, of which *E. blasius* is considered a junior subjective synonym. Therefore, in the absence of credible syntypes of *E. blasius*, there is an exceptional need for the neotype to define this taxon objectively due to its almost certainly incorrect type locality, "Cuba," and currently unrecognized species present among its relatives. Hereby, N.V.G. designates the specimen in MFNB illustrated in Fig. 72a (DNA sample NVG-24028D10) as the **neotype** of *Eudamus blasius* Plötz, 1881. This neotype corroborates the current and long-standing treatment of the name as a junior subjective synonym of *Telegonus (Rhabdoides) elorus* (Hewitson, 1867) (Godman 1907; Evans 1952; Mielke 2005) and thus stabilizes nomenclature as it is applied today.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *E. blasius*, which is necessary because a new species is

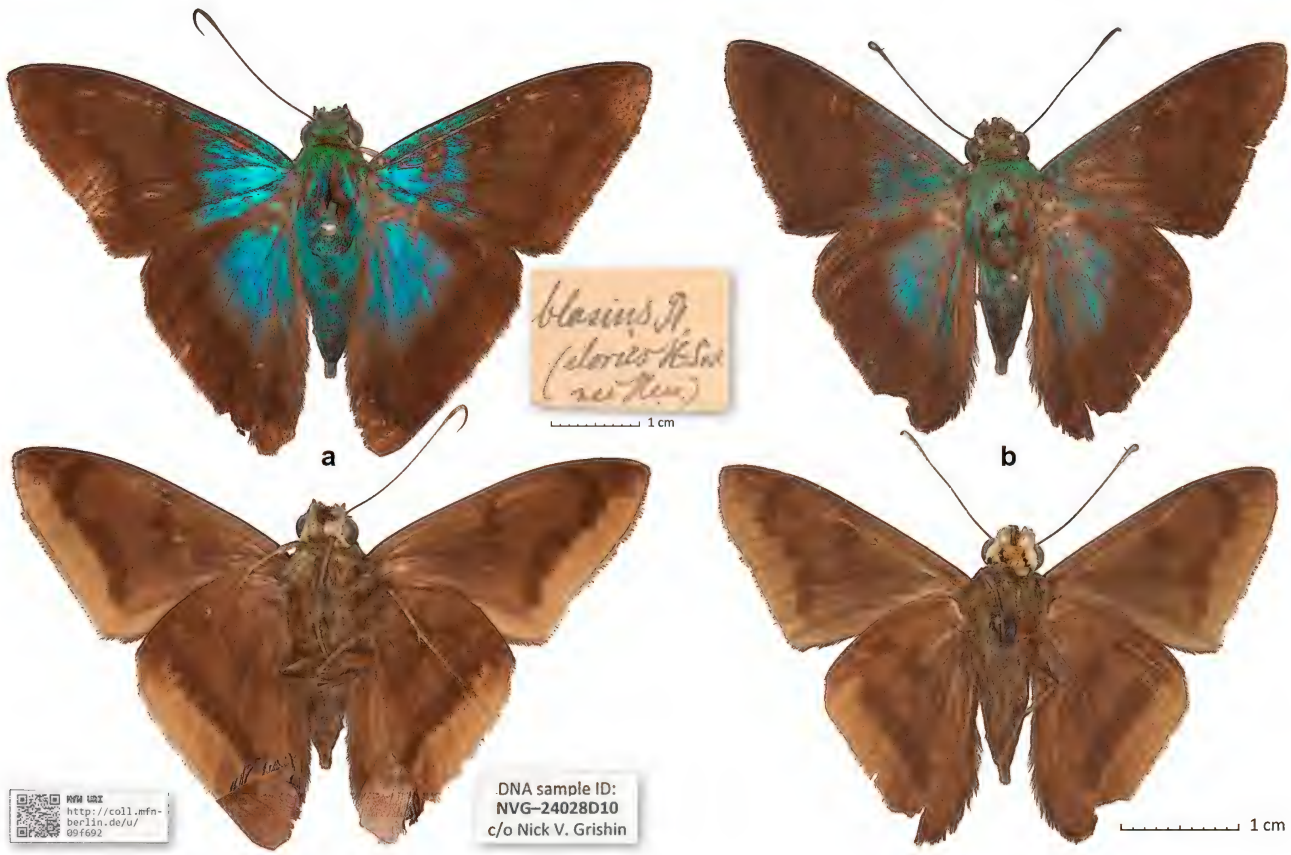


Fig. 72. Type specimens of *Telegonus* (*Rhabdoides*) in dorsal (top) and ventral (bottom) views, data in text: **a)** neotype of *Eudamus blasius* Plötz, 1881 ♂ NVG-24028D10 with its labels reduced to ¾ of the specimen scale (the scale for labels is below the handwritten label), and **b)** *T.* (*R.*) *elorianus* **sp. n.** holotype ♂ NVG-24028D11, no labels are shown for it.

present among its close relatives; **75.3.2.** The characters to differentiate this taxon from others are stated in the original description (Plötz 1881) and are: the body and wing bases are blue or green above; ventral forewing below without a white spot near mid-costa, brown (not blue) at the base; fringes of the hindwing are narrowly whitish; ventral side of all wings is light brown along the margin and sharply bordered by a dark brown postdiscal band; tornus of the hindwing beneath is shaded dull brown up to vein CuA_2; **75.3.3.** The neotype specimen is a male bearing three labels (1st handwritten, others printed): [blasius Pl. | (elorus H-Sch | nec Hew.)], [DNA sample ID: | NVG-24028D10 | c/o Nick V. Grishin], [{QR Code} MfN URI | http://coll.mfn- | berlin.de/u/ | 09f692] and illustrated in Fig. 72a; the neotype is missing the right antenna and has a tornus repaired from the ventral side on both hindwings; pieces of wings of other specimen(s) glued to the neotype to repair it are hereby excluded from the neotype; **75.3.4.** We failed to find definitive syntypes of *E. blasius* among Hesperiidae holdings in all collections we visited (see Acknowledgments for their list) and, therefore, believe that they were lost, although it is possible that the neotype itself might have been a syntype; **75.3.5.** The neotype agrees with the original description (Plötz 1881) and information about *E. blasius* from other sources (Herrich-Schäffer 1869; Godman 1907), as evidenced by observing the characters of this taxon listed above (75.3.2.) in the neotype photographs (Fig. 72a); **75.3.6.** The neotype is lacking a locality label and the original type locality given as "Cuba" is almost certainly incorrect, thus both the neotype and syntypes are from an unknown locality; and the neotype is a specimen collected around the same time as syntypes, is in the collection where many primary type specimens of Plötz and Herrich-Schäffer are deposited, and might even be a syntype; **75.3.7.** The neotype is in the Museum für Naturkunde, Berlin, Germany (MFNB). As a result of the neotype designation, the type locality of *E. blasius* becomes Southeast or South Brazil, as determined by genomic comparisons, and is to be refined further by sequencing of additional specimens. The COI barcode sequence of the neotype, sample NVG-24028D10, GenBank PV550018, 658 base pairs, is:

AACTCTATATTTTATTTTTGGAATTTGAGCAGGATTAATCGGAACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGACGATCAAATTTATAACACC
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTCTAATAATAGGAGCCCCTGATATAGCTTTTCCACGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTCGAAAATGGTGCTGGTACAGGATGAACAGTTTATCCCCCTCTTTCATCAAATATTGC
CCATCAAGGAGCATCAGTTGACTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATCATTAATATACGAATTAATAACTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTTGGAATTACAGCATTATTATTATTACTTTCACTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACCT
CATTTTTTGATCCAGCGGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Telegonus (*Rhabdoides*) *elorianus* Grishin, new species

http://zoobank.org/F15033DB-BF2C-4B5F-AF48-6025370630A7

(Figs. 61 part, 72b, 89 part)

Definition and diagnosis. Genomic analysis reveals that a specimen from an unknown locality is sister to *Telegonus* (*Rhabdoides*) *elorus* (Hewitson, 1867) (type locality in Brazil, likely Southeast or South), but is genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 2.9% (19 bp). Therefore, this specimen represents a new species. This new species keys (incompletely) to "*Astraptes elorus*" C.14.24 in Evans (1952) but differs from it by less yellow and browner margins of wings beneath and a partly broken into spots (not entire) dark postdiscal band on ventral forewing. This species may not be cryptic, but due to unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly3014.2.4:T387A, aly17.7.2:T583C, aly17.7.2:C585T, aly166.2.1:T183A, aly166.2.1:T216A, aly1121.5.5:C102C (not A), aly1139.14.2:T75T (not C), aly221.16.17:C171C (not T), aly221.16.17:G174G (not A), aly770.12.2:G778G (not C); and COI barcode: T136C, T355T (not A), C478T, A451T, C595C (not T).

Barcode sequence of the holotype. Sample NVG-24028D11, GenBank PV550019, 658 base pairs:

AACTCTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGCGATGATCAAATTTATAATACT
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCTCTAATAATAGGAGCCCCTGATATAGCTTTCCCACGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCACCAAGGAGCATCAGTTGACTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAACTTAAATACTT
CATTTTTTGACCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 72b, bears the following six rectangular labels (first two handwritten, others printed), five white: [Blasius | Plötz. ~~no 56~~ | taf. 93], [14:12.], [Coll. Weymer], [DNA sample ID: | NVG-

24028D11 | c/o Nick V. Grishin], [{QR Code} MfN URI | http://coll.mfn- | berlin.de/u/ | 09c7b8], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | elorianus Grishin]. On the first label, "taf[el]. 93" refers to the number of an unpublished drawing of *Eudamus blasius* Plötz, 1881 (type locality given as "Cuba", likely in Southeast or South Brazil) by Plötz (1881). The label [14:12.] corresponds to the number for *Telegonus blasius* in Mabille's catalog (1903).

Type locality. Not stated on the labels of the holotype, likely in Southeast or Southern Brazil.

Etymology. The name is formed from the name of its sister species, *T. elorus*, and is a noun in apposition.

Distribution. Currently unknown, likely in Southeast and Southern Brazil.

Telegonus (*Rhabdoides*) *perumazon* Grishin, new species

http://zoobank.org/528BEF25-DCF4-41D3-B4B9-4195F6AC1E24

(Figs. 61 part, 73, 74a–b, 89 part)

Definition and diagnosis. Genomic analysis reveals that a mostly brown specimen from southeastern Peru with prominent blue wing bases above and a large white ventral forewing tornal area is (unexpectedly) sister to a more yellow-toned and darker on ventral forewing species that Steinhauser identified as "*Astraptes weymeri*" (actually a new species described below), but is genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 3.8% (25 bp). Therefore, the Peruvian specimen represents a new species. This new species keys to "*Astraptes chiriquensis oenander*" C.14.30(d) in Evans (1952). Evans misidentified *Eudamus oenander* Hewitson, 1876, and Evans's "*oenander*" corresponds in part to the species we identify as *Telegonus creteus* (Cramer, 1780) (type locality in Suriname). The new species differs from its relatives by a combination of the following characters: wings are rounder than in some other species. i.e., the hindwing is not lobed and has a convex outer margin; both sides of the forewing and the ventral hindwing have well-developed dark bands that strongly stand out from the paler ground color; basal third to half of wings and body above are with blue (rather than green) scales, ventral forewing has a very broad and rather round pale tornal spot that is merged with the inner margin but does not enter the discal cell, which is brown; the costal margin of the ventral forewing is brown, not paler than the ground color and bluish only at the base; the ventral hindwing is not paler by the margin and richly overscaled with yellowish scales (except the dark brown bands). Due to unexplored individual variation of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly2752.2.4: A177T, aly2752.2.4:T153C, aly1349.6.4:G40C, aly18312.2.2:A531G, aly18312.2.2:C647G, aly250.4.1: C153C (not T), aly250.4.1:A189A (not C), aly506.7.6:G198G (not A), aly506.7.6:C166C (not A), aly839.26. 4:T811T (not C). The COI barcode does not distinguish this species, likely due to introgression. Although it is closest to *T. weymeri* in the nuclear genome, this new species possesses a mitochondrial genome

Fig. 73. *Telegonus* (*Rhabdoides*) *perumazon* **sp. n.** holotype ♂ NVG-14111C12 in dorsal (left) and ventral (right) views.

Fig. 74. Male genitalia of *Telegonus* (*Rhabdoides*) holotypes (unless indicated), data in text: **a–b)** *T. perumazon* **sp. n.** NVG-14111C12; **c–g)** *T. steinhauseri* **sp. n.** NVG-23063E11; **h–l)** *T. chiapus* **sp. n.** NVG-23063G01; **m–o)** *T. chiapus* **sp. n.** paratype NVG-24064A06; **p–t)** *T. colotrix* **sp. n.** NVG-23063G02; **u–v)** *T. sobrasus* **sp. n.** NVG-19071H11 in different views: **a**, **c**, **e**, **h**, **j**, **o**, **p, r, u)** left lateral; **b**, **d**, **i**, **n**, **q**, **v)** dorsal; and **f, g, k–m, s, t)** right lateral: **a, b, m–o, u, v)** complete genital capsule and **c**, **d**, **h**, **i**, **p, q)** genitalia with **e**, **j**, **r)** aedeagus (vesica everted, cornuti on the right) and **f**, **k**, **s)** right and **g**, **l**, **t)** left valvae detached and shown separately. Beige arrows connect different views or parts of the same genitalia.

nearly identical to *Telegonus erana* (Evans, 1952), **stat. nov.** and some specimens of *Telegonus grullus* (Mabille, 1888), **stat. rest.** (see below for the justification of the species status) (Fig. 61c). Therefore, COI barcodes cannot be relied upon for identification purposes.

Barcode sequence of the holotype. Sample NVG-14111C12, GenBank PV550020, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATCGGAACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGACGATCAAATTTATAACACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCATTAATAATAGGAGCTCCTGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGACTTCTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCACCAAGGAGCATCAGTTGATTTAGCTATTTTTTCCCTACATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATAAAAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTATGAGCTGTTGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCAGGAGGAGGAGACCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 73 (genitalia Fig. 74a, b), bears the following five printed (text in italics handwritten) rectangular labels, four white: [PERU:MD 491m | Amazonia Lodge *2568* | 16.V.2012 Kinyon], [DNA sample ID: | NVG-14111C12 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E10 | c/o Nick V. Grishin], [genitalia: | NVG240817-49 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | perumazon Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Type locality. Peru: Madre de Dios, Amazonia Lodge, elevation 491 m.

Etymology. The name signifies the distribution of this species in the Amazonian region of Peru: *Peru* + [A]*mazon*, and is treated as a masculine noun in apposition.

Distribution. Currently known only from the holotype collected in southeastern Peru.

Lectotype designation for *Telegonus chiriquensis* Staudinger, 1875

Telegonus chiriquensis was described from a series of several males and females collected by Heinrich Ribbe in Chiriquí, Panama, with a single ("somewhat differing") specimen from Panama, Panama (Staudinger 1875). Furthermore, Staudinger illustrated *T. chiriquensis* in a later publication (Staudinger 1884–1888). We located syntypes of this species in MFNB (3♂♂ and 2♀♀ labeled as "Origin.") and ZSMC (1♂ and 1♀ labeled as "Paratype"). Genomic sequencing of several syntypes reveals that the type series of *T. chiriquensis* is polytypic and consists of at least two species not most closely related to each other (Fig. 61). Phenotypic inspection confirms this conclusion. One specimen (sequenced as NVG-15031B10, Fig. 75d), which bears the largest number of labels, including "chiriquensis Stgr" (likely in Staudinger's handwriting), "bifascia H. S" (possibly in Hewitson's handwriting), "Lectotypus" (probably added by or by the request of Olaf H. H. Mielke), and "LECTOTYPE ♂ Telegonus | chiriquensis | Staudinger, 1875 | designated by: S.R. Steinhauser" (added by Steinhauser), is a male conspecific with *Thymele grullus* Mabille, 1888 (type locality in Panama: Chiriquí, lectotype sequenced as NVG-15031B12), as evidenced by genomic sequencing (Fig. 61). A lectotype designation has not been published for *T. chiriquensis*, however, Steinhauser (1987) wrote: "I have examined a syntype of this … taxon from the type series in the ZMHU which I will designate as lectotype in a future paper" referring to this syntype NVG-15031B10 in MFNB. Other syntypes of *T. chiriquensis* belong to a species that has been referred to as *chiriquensis* in most literature, e.g., in Evans (1952).

It is unclear why Steinhauser decided to designate this syntype, which is not conspecific with the rest of the type series, as the lectotype. It is possible that it was the only syntype he inspected, not seeing others. This syntype was likely the only one mailed to Steinhauser from Berlin. We believe that Steinhauser worked with this syntype in Sarasota, FL, USA (the Allyn Museum of Entomology location) and not in Berlin, because this specimen carries a label "Allyn Museum Photo No. *89/2/3/16,17 900102/1,2*" with numbers in italics in Steinhauser's handwriting indicating that the photo may have been taken in Sarasota, and also a label "Zool. Mus. Berlin", likely added by Steinhauser to keep track of loaned specimens. This syntype was probably selected to be mailed to Sarasota because it was the first one in the series (top left, right below the header label with the name "chiriquensis | Staudinger") and has accumulated the largest number of labels, including the identification label "chiriquensis Stgr".

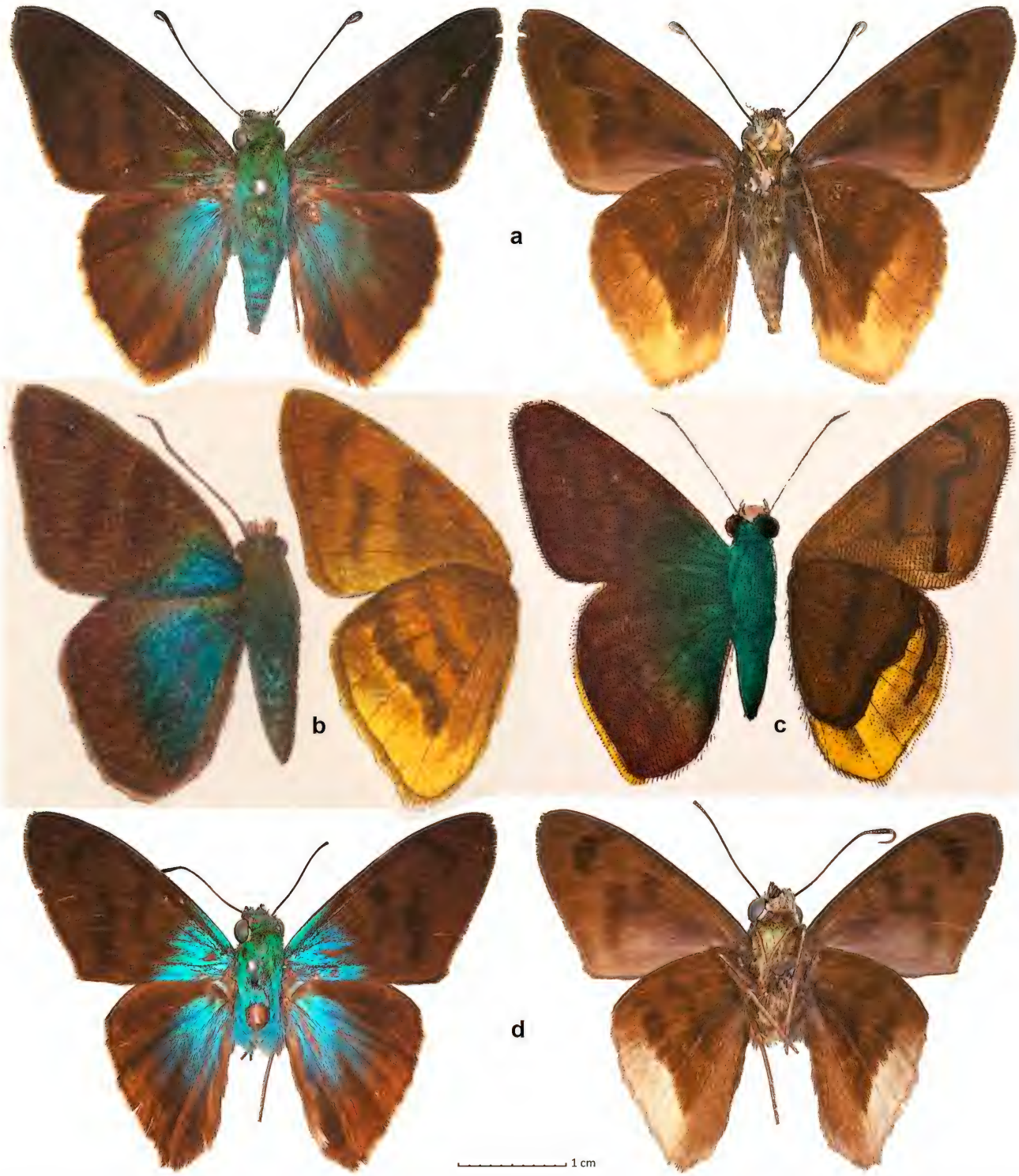


Fig. 75. *Telegonus chiriquensis* and relatives in dorsal (left) and ventral (right) views: **a)** lectotype of *Telegonus chiriquensis* designated herein, NVG-24028C04, data in text; **b)** illustrations of *T. chiriquensis* from Draudt (1922); **c)** illustration of *T. chiriquensis* from Staudinger (1884–1888); **d)** a paralectotype ♂ of *T. chiriquensis* that is not conspecific with the lectotype and is *T. grullus* from Panama: Chiriquí, Ribbe leg., NVG-15031B10 [MFNB]; **a)** and **d)** photographed by Bernard Hermier.

All other syntypes in MFNB, the collection with the largest number of syntypes, only have the following three labels: “Origin.”, “Chiriqui | Ribbe”, and “Paralectotypus”, except one of the females with an additional label “Telegonus | chiriquensis” indicating that this was the specimen loaned to Godman and Salvin (1893) as mentioned in their book: “Dr. Staudinger has kindly lent us his type of this species, and

also a male, which he considered to belong to *T. elorus* of Hewitson." Handwriting on this identification label is consistent with that of Godman. A similar-styled label written by the same person is placed on the lectotype of *T. grullus*, about which Godman and Salvin (1893) wrote: "the type lent us by Dr. Staudinger". From these considerations, we deduce that the female syntype with the label "Telegonus | chiriquensis" was considered to be "his type" of this species by Staudinger. On the one hand, mentioning this female as "type" by Godman and Salvin (1893) does not constitute a lectotype designation according to the ICZN Code Art. 74.6. because the original description of *T. chiriquensis* mentions more than one specimen, implying that the name was proposed from a series of syntypes (Staudinger 1875). On the other hand, it was Godman and Salvin (1893), and not Mielke and Casagrande (2002), who designated a lectotype of *T. grullus* by referring to "the type" (Art. 74.6.) because the original description had no implications about the number of specimens involved (Mabille 1888). Both designations refer to the same specimen. In summary, our analysis suggests that Staudinger considered the species that is not *T. grullus* to represent his concept of *T. chiriquensis* better.

This is further evidenced by an illustration of *T. chiriquensis* in the book that he authored and co-edited (Staudinger 1884–1888). This illustration, reproduced here in Fig. 75c, is particularly similar to one of the male specimens in the MFNB collection that is also not *T. grullus*. The two species can be told apart by the color of the ventral hindwing from the vein 1A+2A to the inner margin (anal fold). The anal fold beneath is entirely brownish in *T. grullus* (Fig. 75d right), while it is partly yellow towards the tornus in the other species (Fig. 75a–c right). Staudinger's illustration shows an entirely yellow tornus up to the inner margin (Fig. 75c right), allowing unambiguous selection of the illustrated species from the type series of *T. chiriquensis*. Moreover, broader wing shape and more interconnected ventral forewing dark bands agree better with the species that is not *T. grullus*. Furthermore, Staudinger's illustration shows a brown patch directed toward the tornus within the yellow area along the vein 1A+2A on the ventral hindwing. Only one of the syntypes possesses this patch and otherwise agrees best with the illustration.

Finally, the illustrations of *T. chiriquensis* in Draudt (1922), reproduced here in Fig. 75b, do not depict *T. grullus* either, but it is not clear whether they—ventral and dorsal side, possibly of two different specimens due to the wing shape difference: male (ventral) and female (dorsal)—show syntypes or even specimens conspecific with the syntypes of *T. chiriquensis*. It is conceivable that they are copies of Plötz's unpublished and possibly lost drawing t. 1342 (Godman 1907) of *A. weymeri*, which was regarded as a junior subjective synonym of *T. chiriquensis* by Draudt (1922). For all these reasons, we arrived at the conclusion that this "future lectotype" inspected by Steinhauser (which is *T. grullus*) is not the best choice to represent Staudinger's concept of *T. chiriquensis*. We believe that both the historical accuracy (i.e., selecting the species dominant in the type series, which is also the species illustrated in a book by the author of this taxon) and the stability of nomenclature (i.e., the species that has been regarded as *T. chiriquensis* in the most widely accepted works since the original description, such as Godman and Salvin (1893) and Evans (1952), in part) would be served better by designating a specimen different from the one inspected by Steinhauser as the lectotype of *T. chiriquensis*.

Therefore, to stabilize nomenclature and to select one species out of the polytypic type series, N.V.G. hereby designates a syntype in the MFNB collection, a male illustrated in Fig. 75a and bearing the following five rectangular labels (1st purple, 3rd red, others white): [Origin.], [Chiriqui | Ribbe], [Paralectotypus], [{QR Code} http://coll.mfn-berlin.de/u/ | e1f9d5], and [DNA sample ID: | NVG-24028C04 | c/o Nick V. Grishin] as the **lectotype** of *Telegonus chiriquensis* Staudinger 1875. The lectotype has a scar on its right forewing dorsal side starting from a chipped outer margin near the apex, directed towards the middle of the inner margin, and reaching the vein CuA_1. The lectotype (Fig. 75a) resembles Staudinger's illustration (1884–1888) (Fig. 75c) more than paralectotypes in MFNB (e.g., Fig. 75d). Moreover, our choice of the species to be selected from the type series as *T chiriquensis* also makes better use of existing names. If the syntype of *T. chiriquensis* that is conspecific with *T. grullus* is selected as the lectotype, then *T. grullus* would become a junior subjective synonym of *T. chiriquensis*, but the second species represented by several syntypes of *T. chiriquensis* would not have an available name associated with it and would become a "new" species that needs a name. However, this second species is

prevalent in the type series (only one former syntype is conspecific with *T. grullus*) and, as we discussed above, Staudinger and subsequent literature, including Evans (1952) (in part), regarded this prevalent species as *T. chiriquensis*. The COI barcode sequence of the lectotype, sample NVG-24028C04, GenBank PV550021, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAGATTACTCATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACC
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTCCCATTAATAATAGGAGCCCCTGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCGTCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCCCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGATTTAGCTATTTTTTCCTTACATTTAGCTGGTATTTCCTCTATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCATTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCACTACCAGTTTTAGCAGGAGCTATTACCATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGGGGAGGAGATCCAATTTTATACCAACATTTATTT

Lectotype designation for *Aethilla weymeri* Plötz, 1882

Aethilla weymeri Plötz, 1882 was described from an unstated number of specimens of unknown provenance (Plötz 1882b). Being absent from the 1876 version in the ZSMC library, this species was added to the manuscript near its publication. Furthermore, Plötz did not specify the number of his drawing for *A. weymeri* and instead stated "Nachtr." meaning Nachtrag (supplement). It is possible that the drawing was not made at the time of publication. Later, this drawing was given the number 1342, as specified by Godman (1907), who stated that the illustrated specimen was from Chiriquí and selected a specimen from his collection that agreed best with the illustration. This specimen in BMNH bearing a label "Compared with Plotz's drawing of weymeri, Plötz" may serve as a proxy for the lost drawing. It is from Tabasco, Mexico, and has broadly yellow submarginal areas on the ventral hindwings but dark (not yellow, as per the original description) fringes and brighter cyan-blue (rather than dark green in the description) dorsal overscaling. Images of this specimen, photographed by N.V.G., are shown on the Butterflies of America website (Warren et al. 2024).

To learn more about *A. weymeri*, we searched for its syntypes in MFNB, where the Weymer collection is deposited. We reason that Plötz proposed the name to honor Weymer, who might have discovered this species. We found two specimens that match the original description of *A. weymeri* rather well, e.g., they have dark green (not blue) overscaling at wing bases and body above, pale yellowish-gray palpi beneath, orange-yellow fringes on the hindwing, and a yellow outer marginal area on the ventral hindwing broadest at the tornus. Both specimens bear a label with the name "victa": "victa m il" and "victa Wmr il." suggesting that Weymer considered these specimens to be a new species that he wanted to name "victa". On the first specimen, "m" stands for "mihi" (Latin for "of me"), placed after a species name as an attribution of the new species to the writer. This notation was common over a century ago, instead of the author's name being written directly. On the second specimen, Weymer used the abbreviation of his last name "Wmr". On both specimens, "il" is for "in litteris," meaning that the name has not been published. Moreover, a label on the first specimen states "n sp. 462 Plötz", and we interpret it as indicating that Plötz considered the specimen number 462 in Weymer's collection to be a new species.

Fig. 76. Lectotype of *Aethilla weymeri* Plötz, 1882 NVG-24028C11 in dorsal (left) and ventral (right) views, data in text.

The first specimen does not have a locality label. The second specimen bears a label "Central Amer" and collection year 1887. The second specimen was collected after the description of *A. weymeri* in 1882 and, therefore, cannot be a syntype. However, we consider the first specimen to be a syntype of *A. weymeri*, because it matches the original description well, is from Weymer's collection (thus proposing a patronym would make sense), and has been regarded by Plötz as a new species. We hypothesize that Plötz inspected Weymer's collection and told him this specimen represented a new species. Weymer decided to propose a name "victa" for it. However, this name was not published by Weymer, but Plötz added this species into his key as "weymeri" right before publication. The syntype did not have a locality label, and Plötz could not have stated the locality of *A. weymeri* in his publication. However, later, the second specimen of "victa" was collected in Central America, and when Plötz was preparing the drawing, he listed the locality as "Chiriqui". It is possible that other specimens of "victa" with the locality "Chiriqui" also existed, and maybe they were illustrated by Plötz instead of the syntype.

To stabilize nomenclature and define the name *A. weymeri* objectively, N.V.G. hereby designates this found syntype in the MFNB collection illustrated in Fig. 76 and bearing the following six labels (1st, 2nd, and 3rd handwritten, others printed): [462 | Weymer], [victa m il | n sp. 462 Plötz], [? Aethilla], [Coll. Weymer], [{QR Code} http://coll.mfn-berlin.de/u/ | 44a098], [{QR Code} MfN URI | http://coll.mfn- | berlin.de/u/ | 09f692], [DNA sample ID: | NVG-24028C11 | c/o Nick V. Grishin] as the **lectotype** of *Aethilla weymeri* Plötz, 1882. The first three labels are in Weymer's handwriting. The lectotype is missing the club of the left antenna, its right antenna overlays the forewing on the dorsal side, and the tornus of its right hindwing is repaired; pieces of wings of other specimen(s) glued to the lectotype to repair it are hereby excluded from the lectotype. The type locality of *A. weymeri* is likely in Panama: Chiriquí (Godman 1907). Consistently, genomic sequencing places the lectotype among specimens from Central America. The COI barcode sequence of the lectotype, sample NVG-24028C11, GenBank PV550022, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAGATTACTCATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACC
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTCCCATTAATAATAGGAGCCCCTGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCGTCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCCCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGATTTAGCTATTTTTTCCTTACATTTAGCTGGTATTTCCTCTATTCTTGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCATTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCACTACCAGTTTTAGCAGGAGCTATTACCATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGGGGAGGAGATCCAATTTTATACCAACATTTATTT

Aethilla weymeri Plötz, 1882 is a junior subjective synonym of *Telegonus* (*Rhabdoides*) *chiriquensis* Staudinger, 1875

Genomic phylogeny of *Telegonus* (*Rhabdoides*) Scudder, 1889 (type species *Eudamus cellus* Boisduval & Le Conte, [1837]), reveals that the lectotype of *Aethilla weymeri* Plötz, 1882 (type locality not stated, likely in Panama: Chiriquí, sequenced as NVG-24028C11) is placed among specimens of *Telegonus* (*Rhabdoides*) *chiriquensis* Staudinger, 1875 (type locality in Panama: Chiriquí, lectotype sequenced as NVG-24028C04) (Fig. 61). Therefore, we propose that *Aethilla weymeri* Plötz, 1882 is a junior subjective synonym of *Telegonus* (*Rhabdoides*) *chiriquensis* Staudinger, 1875, as regarded by Evans (1952).

Telegonus (*Rhabdoides*) *steinhauseri* Grishin, new species

http://zoobank.org/D916455A-197F-41FF-A0B5-1C2711054FDC

(Figs. 61 part, 74c–g, 77, 89 part)

Definition and diagnosis. This is the species Steinhauser (1987) identified as "*Astraptes weymeri*." However, the lectotype of *Aethilla weymeri* Plötz, 1882 (type locality not stated in the original description, likely in Panama: Chiriquí) reveals that it is a junior subjective synonym of *Telegonus* (*Rhabdoides*) *chiriquensis* Staudinger, 1875 (type locality in Panama: Chiriquí), and this species is left without a name and is therefore new. In the nuclear genome trees, it is sister to *T. perumazon* **sp. n.** and is genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 3.8% (25 bp), and facies differ by reduced pale coloration by the ventral forewing tornus and more extensive yellow overscaling in the ventral hindwing submarginal area. This new species keys to "*Astraptes chiriquensis chiriquensis*" C.14.30a in Evans (1952) and was included by him in that taxon. However, it differs from

Fig. 77. *Telegonus* (*Rhabdoides*) *steinhauseri* **sp. n.** holotype ♂ NVG-23063E11 in dorsal (left) and ventral (right) views.

T. chiriquensis by a larger greenish-blue area (bluer rather than greener) at the base of the dorsal forewing nearly reaching the discal dark band even near the costal margin; the yellow submarginal area of the ventral hindwing being stronger overscaled with brown (especially around the tornus and apex) or nearly all brown and only slightly paler than the rest of the wing; and the middle dark band on the ventral hindwing being shifted towards the discal band rather than the subapical band. Although this species may not be cryptic, in DNA, a combination of the following base pairs is diagnostic in the nuclear genome: aly250.4.1:C153T, aly250.4.1:A189C, aly971.19.1:T190C, aly971.19.1:T1341G, aly971.19.1:C2602T; and COI barcode: A34G, T49C, 508G, 596T.

Barcode sequence of the holotype. Sample NVG-23063E11, GenBank PV550023, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGGTTAATTGGAACCTCCTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTCCCATTAATAATAGGAGCCCCTGATATAGCTTTTCCTCGTA
TGAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCCGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGATCTAGCTATTTTCTCTTTACATTTAGCTGGTATTTCTTCTATTCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTGTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 77 (genitalia Fig. 74c–g), bears the following nine printed (text in italics handwritten) labels (2nd triangular, others rectangular), seven white: [MEXICO: VERACRUZ | Catemaco | *X.*1972 | T. Escalante], [>, a piece of antenna is glued to this label, no text, [A. C. Allyn | Acc. 1973-48], [MGCL/FLMNH | Specimen no. | 16820], [Genit. Vials | SRS-*1836*], [Telemachus weymeri | (Plötz, 1882) ♂| Det. S.R. Steinhauser], [DNA sample ID: | NVG-23063E11 | c/o Nick V. Grishin], one pink without any text, and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | steinhauseri Grishin]. **Paratypes:** 5♂♂ and 5♀♀: Mexico: Veracruz: 1♀ NVG-14082D02 Presidio, Jun-1942, T. Escalante leg. [AMNH] and 1♀ NVG-18027G11 Santa Rosa, Aug-1906, Wm. Schaus collection [USNM]; and Oaxaca, Candelaria Loxicha, > 500 m, E. C. Welling leg.: 1♂ NVG-14082D03 7-Nov-1971 genitalia SRS-1702 [AMNH]; 1♀ NVG-23063E07 2-Oct-1969 genitalia SRS-879 [MGCL]; and 1♀ NVG-23063E08 4-Oct-1969 [MGCL]; 1♂ NVG-23063E12 Guatemala, Santa Rosa, El Naranho, 25-Jun-1925, ex coll. E. Le Moult, genitalia SRS-864 [MGCL]; 1♂ NVG-19075B01 Honduras, old. Edw. T. Owen collection, genitalia SRS-1838 [USNM]; and Panama [USNM]: Canal Zone, Farfan, S. S. Nicolay leg.: 1♂ NVG-14105A01, 14-Feb-1963 and 1♀ NVG-14105A02, 15-Feb-1963 and 1♂ NVG-19075B04, USNMENT 01588551 Herrera, Cerro Alto Higo, 1000 m, 23-Dec-1984, G. B. Small leg.

Type locality. Mexico: Veracruz, Catemaco.

Etymology. The name, a noun in the genitive case, honors Stephen R. Steinhauser, who made significant contributions to our knowledge of Hesperiidae and had a keen interest in *Telegonus* but did not have an opportunity to search for syntypes in Berlin and, therefore, did not recognize this species as new.

Distribution. From southern Mexico to Colombia and Venezuela.

Comment. We list data on all labels of the holotype, verbatim, including identification labels. One of such labels contains an unpublished name “Telemachus.” Here, we use Art. 8.3. of the ICZN Code and

disclaim the name "Telemachus" for nomenclatural purposes. Thus, we consider this name to be unpublished. Furthermore, we note that the unavailable infrasubspecific name *Telegonus chiriquensis* form *godmani* Williams, 1927 (see discussion of names by Williams in Zhang et al. (2022b)) refers to specimens most likely conspecific with this species.

Telegonus erana (Evans, 1952) and *Telegonus meretrix* (Hewitson, 1876) are species distinct from *Telegonus chiriquensis* Staudinger, 1875

Genomic analysis reveals that *Telegonus chiriquensis erana* (Evans, 1952) (type locality in Ecuador: Balzapamba) and *Telegonus chiriquensis meretrix* (Hewitson, 1876) (type locality in Ecuador) currently treated as subspecies of *Telegonus chiriquensis* Staudinger, 1875 (type locality in Panama: Chiriquí, lectotype sequenced as NVG-24028C04) are not monophyletic with it and belong to two different clades being strongly differentiated from it genetically (Fig. 61): e.g., COI barcodes in the closest pair (*T. chiriquensis erana* and *T. chiriquensis chiriquensis*) differ by 4.1% (27 bp). *Telegonus chiriquensis meretrix* belongs to a different species group and is closer related to *Telegonus parmenides* (Stoll, 1781), **stat. rest.** and not to *Telegonus creteus* (Cramer, 1780) as the other two taxa (Fig. 61). *Telegonus chiriquensis meretrix* is characterized by the blue area on the dorsal forewing reaching the discal brown band (especially along the costal margin) and broad ventral forewing bands. These characters are shared with *Telegonus cretatus* Hayward, 1939 (type locality also in Ecuador) from the same species group, among several other species, rather than with *T. chiriquensis*, which has reduced blue-green bases of the forewings. Evans (1952) misidentified *E. meretrix* in part, and except for three females from Ecuador (with broad blue wing bases), other specimens (with narrow blue-green bases) belong to other species (one described below as new), indeed, closely related to *T. chiriquensis*. For these reasons, we propose that *Telegonus erana* (Evans, 1952), **stat. nov.** and *Telegonus meretrix* (Hewitson, 1876), **stat. rest.** are species distinct from *Telegonus chiriquensis* Staudinger, 1875.

Telegonus (*Rhabdoides*) *chiapus* Grishin, new species

http://zoobank.org/0A995D2A-A171-4311-A9E1-379669B6CC44

(Figs. 61 part, 74h–o, 78, 89 part)

Definition and diagnosis. A male from Chiapas, Mexico (in MGCL collection) that resembles *Telegonus chiriquensis* Staudinger, 1875 (type locality in Panama: Chiriquí) in wing patterns is genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 2.7% (18 bp) and, therefore, represents a new species. This new species keys to "*Astraptes chiriquensis chiriquensis*" C.14.30(a) in Evans (1952) but differs from its males by more extensive yellow coloration on the ventral side: the hindwing with a wider brownish-yellow marginal and tornal area, more weakly overscaled with

Fig. 78. *Telegonus* (*Rhabdoides*) *chiapus* **sp. n.** holotype ♂ NVG-23063G01 in dorsal (left) and ventral (right) views.

the ground brown color and more extensively so only towards the apex, and prominent yellowish areas by the forewing tornus and inner margin and some overscaling in the postdiscal area; and more bluish, rather than greenish, overscaling on wing bases and body above, this overscaling is more restricted to the wing base, especially on the hindwing (but occupies nearly half of the hindwing in *T. chiriquensis*). Due to unexplored individual variation in this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly619.2.3:T81C, aly619.2.3: C83T, aly619.2.3:A84G, aly276378.2.2:G167A, aly276378.2.2:T300C; and COI barcode: T385C, T442C, T472C, T499A, T568C, T622C.

Barcode sequence of the holotype. Sample NVG-23063G01, GenBank PV550024, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATCGGAACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCATTAATAATAGGAGCTCCTGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCGTCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCCCTTTCATCTAATATTGC
CCACCAAGGAGCATCAGTTGACTTAGCTATTTTTTCTTTACATTTAGCTGGTATTTCTTCTATTCTTGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATCAATAATTTATCT
TTTGATCAAATACCATTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCCATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCCGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 78 (genitalia Fig. 74h–l), bears the following eight printed (text in italics handwritten) rectangular labels (5th pale-blue, last red, and others white): [MEXICO: CHIAPAS | San Antonio | 4000'; sta. #4 | *8-VIII.* 197*4* | R. Wind], [Genit. Prep. SRS-*856*], [A. C. Allyn | Acc. 1974-24], [SRS Database | No. *673*], [PARATYPE | *Telemachus* | *draudti* | S. R. Steinhauser], [MGCL/FLMNH | Specimen no. | 16922], [DNA sample ID: | NVG-23063G01 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Telegonus (Rhabdoides) | chiapus Grishin]. **Paratypes:** 2♂♂ from Mexico, Chiapas [MGCL]: Selva Negra, 1700 m, Aug-1987, J. de la Maza E. leg.: 1♂ NVG-24064A04 and 1♂ NVG-24064A06 (leg DNA extraction, sequenced), NVG-24101A01 (abdomen DNA extraction and dissection), genitalia NVG241220-23 (Fig. 74m–o).

Type locality. Mexico: Chiapas, San Antonio, elevation 4000'.

Etymology. The name is formed from the name of the Mexican state with the type locality. The name is treated as a masculine noun in apposition.

Distribution. Currently known only from Chiapas, Mexico.

Comment. We list data on all labels of the holotype, verbatim, including identification labels. One of such labels contains an unpublished name "Telemachus draudti", but according to our sequencing results, this specimen is not conspecific with the intended "holotype" of this name. To avoid further confusion, we use Art. 8.3. of the ICZN Code and disclaim the name "Telemachus draudti" for nomenclatural purposes. Thus, we consider this name to be unpublished.

Telegonus (*Rhabdoides*) *colotrix* Grishin, new species

http://zoobank.org/2148CD01-73EB-4D19-A482-EE1668D2F814

(Figs. 61 part, 74p–t, 79, 81a–b, 89 part)

Definition and diagnosis. Sequencing of several specimens from western Colombia that are phenotypically similar to *Telegonus chiriquensis* Staudinger, 1875 (type locality in Panama: Chiriquí) and less so to *Telegonus meretrix* (Hewitson, 1876), **stat. rest.** (type locality in Ecuador) reveals that they are sister to *Telegonus erana* (Evans, 1952), **stat. nov.** (type locality in Ecuador: Balzapamba) and are not monophyletic with *T. chiriquensis* being genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 3.2% (21 bp). Therefore, these specimens represent a new species. This new species keys to "*Astraptes chiriquensis chiriquensis*" C.14.30(a) in Evans (1952) but differs from it and other relatives by broader wings with brown fringes above, the greenish-blue area on the ventral forewing being restricted to the very base, the hindwing area is blue rather than green, ventral forewing dark bands are narrower (especially the subapical short band) and stronger separated from each other, the yellow marginal area on the ventral hindwing is more weakly and evenly overscaled with brown scales even towards the apex and reaches the inner margin near the tornus (the tornal area is brown in *T. erana,* which has green, not blue, wing bases above). The ampulla is knob-like, and only slightly smaller than the dorsal process of the harpe, which is also knob-shaped and directed posterodorsad rather than just dorsad;

Fig. 79. *Telegonus* (*Rhabdoides*) *colotrix* **sp. n.** holotype ♂ NVG-23063G02 in dorsal (left) and ventral (right) views.

the costa is nearly straight (basad of the concavity formed by the rising ampulla) or slightly bisinuate; the harpe is shorter than in relatives and is more rounded terminally, not as pointed as in other species (Fig. 74p–t). Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1395.2.12:A75T, aly2124.2.1:C615T, aly173.39.3:A199T, aly173.39.3:A165G, aly320.15.2:A51T; and COI barcode: A34G, T49T, T206T, T386C, T407T, T508G.

Barcode sequence of the holotype. Sample NVG-23063G02, GenBank PV550025, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGGTTAATTGGAACCTCTTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTCCCATTAATAATAGGAGCCCCTGATATAGCTTTTCCTCGTA
TGAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCCGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGATCTAGCTATTTTCTCTTTACATTTAGCTGGTATTTCTTCTATTCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTGTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 79 (genitalia Fig. 74p–t), bears the following eight printed (text in italics handwritten) rectangular labels (3rd blue, the last red and others white): [COLOMBIA: Cauca; *SUAREZ* | *AREA 1600 m.* | *14/ X /*1974 | No.*CH-145* Coll. | by S.R. y L.M. Steinhauser], [*ASTRAPTES CHIRIQUENSIS* | *CHIRIQUENSIS STDGR.* | ♂| Det: S.R.Steinhauser], [PARATYPE ♂| *Telemachus* | *draudti* | S. R. Steinhauser], [SRS Database | No. *670*], [Genit. Prep. | SRS-*921*], [A. C. Allyn | Acc. 1975-17], [DNA sample ID: | NVG-23063G02 | c/o Nick V. Grishin], [HOLOTYPE ♂ | Telegonus (Rhabdoides) | colotrix Grishin]. **Paratypes:** 1♂ and 2♀♀: Colombia: 1♂ NVG-24028D04 no locality details, old, W. Kalbreyer leg. [MFNB]; 1♀ NVG-14104A03 (leg DNA extraction, sequenced), NVG-23119E11 (abdomen DNA extraction and dissection) Valle del Cauca, 5 km N of Darién, 1500 m, 16-Jan-1988, J. B. Sullivan leg., genitalia NVG240817-50 (Fig. 81a, b) [USNM]; and 1♀ NVG-18027G08, USNMENT 01465202 old, from the Neumögen collection [USNM] with a handwritten label [Telegonus | chiriquensis | Stgr. | chiriqui]. It remains unclear whether "chiriqui" on the label refers to the collecting locality of this specimen or the type locality of *T. chiriquensis*, probably the latter.

Type locality. Colombia: Cauca Department, Suarez area, elevation 1600 m.

Etymology. The name is a fusion of *Colo*[mbia] + [mere]*trix* for this species from Colombia previously misidentified as *T. meretrix*. Furthermore, it is a rather colorful species. The name is treated as a masculine noun in apposition.

Distribution. Currently known from Colombia.

Comment. We list data on all labels of the holotype, verbatim, including identification labels. One of such labels contains an unpublished name "Telemachus draudti", but according to our sequencing results, this specimen is not conspecific with the intended "holotype" of this name. To avoid further confusion, we use Art. 8.3. of the ICZN Code and disclaim the name "Telemachus draudti" for nomenclatural purposes. Thus, we consider this name to be unpublished.

Telegonus (*Rhabdoides*) *flavimargo* Grishin, new species

http://zoobank.org/597C1EFD-5F59-494C-9E23-1E8C549FB043

(Figs. 61 part, 80, 81c–d, 89 part)

Definition and diagnosis. A female from Costa Rica with solid-yellow ventral hindwing margins identified by Steinhauser as "*T. latimargo*" does not group in the Z chromosome tree either with this species or any other pale-margined species of *Telegonus* Hübner, [1819] (type species *Papilio talus* Cramer, 1777). Instead, it is confidently placed as sister to *Telegonus tinda* Evans, 1952 (type locality in Brazil: Pará) (Fig. 61b). In the tree constructed from the autosomes, this female is sister to a clade composed of several species (Fig. 61a). Therefore, it represents a new species. This new species keys to "*Astraptes latimargo bifascia*" C.14.29(a) in Evans (1952) (Evans misidentified both *T. bifascia* and *T. latimargo*, see above) or to "*Astraptes chiriquensis chiriquensis*" C.14.30(a). It differs from *Telegonus grullus* (Mabille, 1888), **stat. rest.** (and this is the species Steinhauser meant by "*latimargo*" in his identification, see below for the justification of the species status) by yellower (vs. whiter) ventral hindwing margins more weakly shaded with brown towards the tornus, a postdiscal dark band on the ventral forewing that is farther from the discal band, and narrower and less prominent ventral forewing dark bands. The new species is sister to *T. tinda* in the Z chromosome and differs from it by bluer rather than greener wing bases and body above and a yellower ventral side with a broad yellow margin lacking in *T. tinda*. It differs from other relatives by the following combination of characters in females: more extensive and bluer than in *Telegonus chiriquensis* Staudinger, 1875 (type locality in Panama: Chiriquí) iridescent area at the base of the dorsal forewing; darker tornal area on the ventral forewing and the submarginal yellow region being the broadest close to the middle of the wing and narrowing towards the tornus; dark postdiscal band on the ventral forewing that is equidistant from the apical and discal bands (not closer to the apical band); more weakly expressed dark bands on the dorsal forewing; and somewhat shorter and not as strongly sclerotized in its anterior half lamella postvaginalis, which has a V-shaped central notch. Due to the cryptic nature of this species (compared to *T. grullus*), most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly128.9.3:G576T, aly770.37.4:C579T, aly54.29.1:A462T, aly54.29.1:T486C, aly2165.5.2:G195A, aly164.11.12:C55C (not T), aly164.11.12:C75C (not T), aly2874.16.4:G81G (not T), aly1196.6.1:C45C (not T), aly671.39.1:A900A (not G); and COI barcode: A34G, T49T, T206C, T407C, T508G.

Barcode sequence of the holotype. Sample NVG-14105A05, GenBank PV550026, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGGTTAATTGGAACCTCTTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTCCCACTAATAATAGGAGCCCCTGATATAGCTTTTCCTCGTA
TGAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCCGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGATCTAGCTATTTTCTCTTTACATCTAGCTGGTATTTCTTCTATTCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTGTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Fig. 80. *Telegonus* (*Rhabdoides*) *flavimargo* **sp. n.** holotype ♀ NVG-14105A05 in dorsal (left) and ventral (right) views.

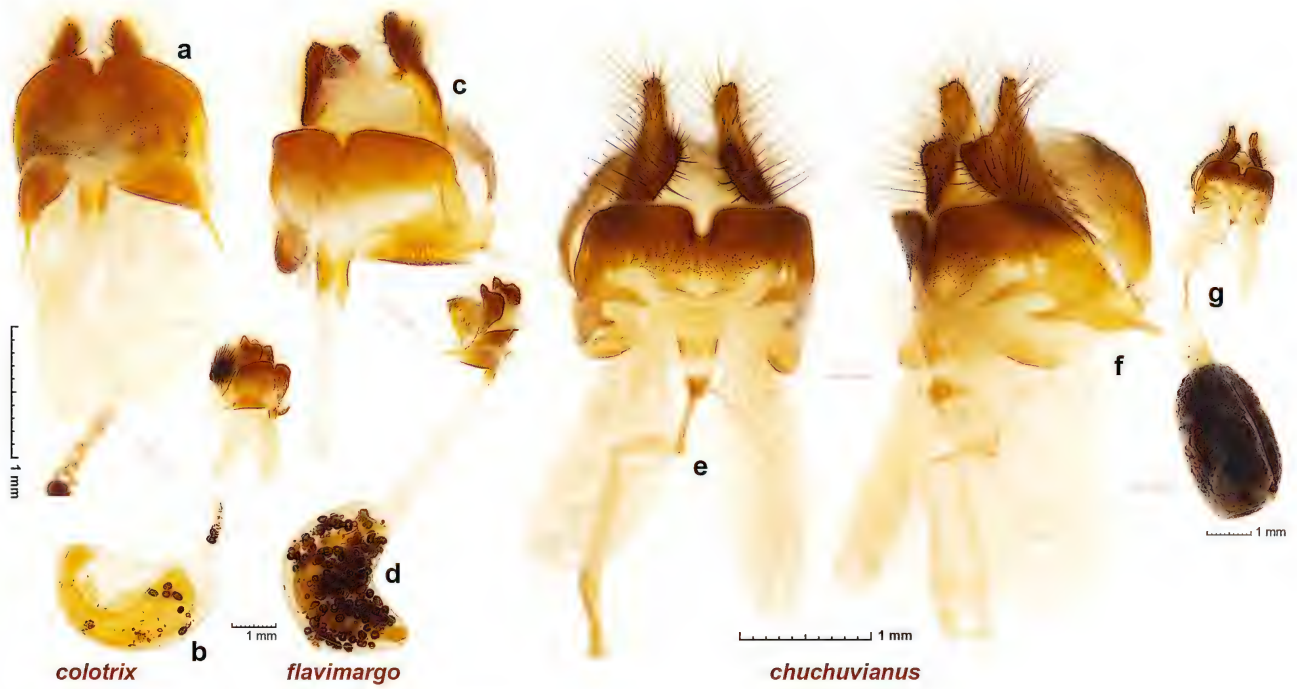


Fig. 81. Female genitalia of *Telegonus* (*Rhabdoides*) holotypes (unless indicated), data in text: **a–b)** *T. colotrix* **sp. n.** paratype NVG-14104A03; **c–d)** *T. flavimargo* **sp. n.** NVG-14105A05; and **e–g)** *T. chuchuvianus* **sp. n.** NVG-24086F12 in **a, c, e, g)** ventral; **b, d)** left ventrolateral; and **f)** right ventrolateral views: **a, c, e, f)** bursa copulatrix omitted and **b, d, g)** complete genitalia shown at 1/3 scale (indicated by smaller scale bars near them). Beige arrows connect different views and magnifications of the same genitalia.

Type material. Holotype: ♀ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 80 (genitalia Fig. 81c, d), bears the following seven printed (text in italics handwritten) rectangular labels, six white: [Guapiles | CR | 850ft.alt], [Collection | WmSchaus], [Telemachus latimargo ♀ | (Herrich-Schäffer, 1869) | Det. S.R. Steinhauser], [DNA sample ID: | NVG-14105A05 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119E12 | c/o Nick V. Grishin], [genitalia: | NVG240817-51 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Telegonus (Rhabdoides) | flavimargo Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Type locality. Costa Rica: Limón Province, Guapiles, elevation 850'.

Etymology. The name is given for the yellow (*flavus* in Latin) marginal area of the ventral hindwing. The name is treated as a masculine noun in apposition.

Distribution. Currently known only from the holotype, female, collected in north-central Costa Rica.

Comment. We list data on all labels of the holotype, verbatim, including identification labels. One of such labels contains an unpublished name "Telemachus." Here, we use Art. 8.3. of the ICZN Code and disclaim the name "Telemachus" for nomenclatural purposes. Thus, we consider this name to be unpublished.

Telegonus (*Rhabdoides*) *sobrasus* Grishin, new species

http://zoobank.org/6783C93A-E535-4D2A-B6E0-EDAFECE13CDE

(Figs. 61 part, 74u–v, 82, 89 part)

Definition and diagnosis. Our analysis (see above) suggests that Evans misidentified *Eudamus oenander* Hewitson, 1876 (type locality in Brazil: Pará). Sequencing of several specimens from South Brazil that

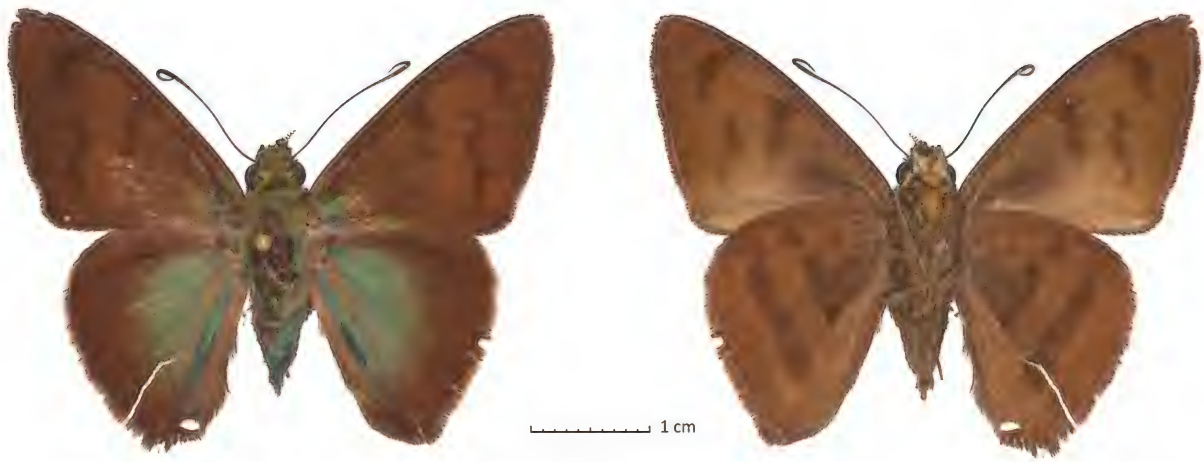


Fig. 82. *Telegonus* (*Rhabdoides*) *sobrasus* **sp. n.** holotype ♂ NVG-19071H11 in dorsal (left) and ventral (right) views.

are within Evans's concept of "*oenander"* reveals that they form a clade sister to *Telegonus creteus* (Cramer, 1780) and are genetically differentiated from it at the species level (Fig. 61) with F_{st}/G_{min}/COI barcode difference of 0.23/0.025/0.9% (6 bp). This new species keys to "*Astraptes chiriquensis oenander*" C.14.30(d) in Evans (1952) (Evans misidentified *Eudamus oenander* Hewitson, 1876) and falls within Evans's concept of this species. The new species is most similar to *Telegonus creteus* (also within Evans's concept of "*oenander*") but differs from it by a shorter and more terminally rounded harpe with a more convex ventral margin in lateral view and a more robust dorsal knob-like process (Fig. 74u), rounder wings in males, more extensive pale overscaling on the ventral forewing and, correspondingly, more contrasting dark bands, which are also more prominent (compared to *T. creteus*) on the dorsal side of wings, a pale brown or yellowish (rather than whitish) and very diffuse tornal area on the ventral forewing, the lack of a green streak along the base of the costal margin on the ventral hindwing, and a more restricted greenish area at the base of the dorsal forewing; and differs from other relatives by the hindwing beneath being dark without a paler submarginal area, only a slightly paler tornal area on the ventral forewing without a defined boundary outlining its, and green (not blue) wings bases above. The ampulla is expanded into a ridge basad reaching half of the valva length, this costa appears bisinuate; the ampulla is separated from the rounded knob-shaped dorsal projection of the harpe by a U-shaped gap (Fig. 74u). Due to the somewhat cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly2487.2.4:G138A, aly2487.2.4:T147C, aly3686.6.3:A183G, aly619.11.3:T21A, aly619.11.3:C40T; and COI barcode: C82C, A244G, T292C, C319C, A562A.

Barcode sequence of the holotype. Sample NVG-19071H11, GenBank PV550027, 658 base pairs:

AACTCTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACCTCTTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTCCCATTAATAATAGGAGCCCCTGATATAGCTTTTCCTCGTA
TGAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATCTCAAGAAGAATTGTTGAAAATGGTGCCGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
CCATCAAGGAGCATCAGTTGATTTAGCTATTTTCTCTTTACATTTAGCTGGTATTTCTTCTATTCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTATGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 82 (genitalia Fig. 74u, v), bears the following six printed (text in italics handwritten) rectangular labels, five white: [BRAZIL:Sta Catarina | Joinville, 0-200m | 26°19'S 48°53'W | *27.XI.1988* | leg. H. Miers], [DNA sample ID: | NVG-19071H11 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119F01 | c/o Nick V. Grishin], [genitalia: | NVG240817-52 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01588534], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | sobrasus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratypes:** 6♂♂ and 2♀♀ from Brazil: Bahia ? (unlabeled specimens, likely historical collection lot no. 4959, two specimens out of three, from either Bahia or Pará), old, Gomez leg. [MFNB]: 1♂ NVG-

24034A01 and 1♀ NVG-24034A02; 1♂ NVG-24028D08 Minas Gerais (no detailed locality), old, R. Haensch S. [MFNB]; Espirito Santo, Leopoldina, 1894 Michaelis leg. [MFNB]: 1♂ NVG-24028C02 and 1♀ NVG-24028E04; 1♂ NVG-24101B03 Paraná, Antonina, Guaricica Ecological Reserve, 15 m, GPS −25.3078, −48.6950, J. A. Shuey & P. Labus leg., genitalia RAA 0761 [MGCL]; and Santa Catarina (no detailed locality) [USNM]: 1♂ NVG-14111D03 Apr-1945, from S. S. Nicolay collection and 1♂ NVG-18027G07, USNMENT 01465201 from B. Neumögen collection, likely around 1900, Genit. Prep. SRS-1049.

Type locality. Brazil: Santa Catarina, Joinville, elevation ca. 50 m, GPS −26.3167, −48.8833.

Etymology. The name is derived from the locality in *So*[uth]+*Bras*[il]+*us* and is treated as a masculine noun in apposition.

Distribution. Eastern and southern parts of Brazil.

Telegonus (*Rhabdoides*) *chuchuvianus* Grishin, new species

http://zoobank.org/54170B26-F116-400F-BFED-C8BE8F1D25E1

(Figs. 61 part, 81e–g, 83, 89 part)

Definition and diagnosis. Inspection of genomic trees reveals that a large female from Chuchuví, Ecuador, is not closely related to any known species of *Telegonus* (*Rhabdoides*) Scudder, 1889 (type species *Eudamus cellus* Boisduval & Le Conte, [1837]), originating at the base of the *parmenides* species group (Fig. 61). Therefore, this female represents a new species. This species is unique in appearance and differs from its relatives by the following combination of characters in females: larger size; blue wing bases and body above; lack of pale spots on the dorsal side of wings; broadly pale-yellowish area on the ventral forewing from CuA_2 to the inner margin (with a brown spot in the middle by the CuA_2 vein and browner area near the outer margin); an unusual pattern on the dark-brown bands on the ventral forewing: the postdiscal band is removed for the subapical band and is vestigial, closer to and fusing with the discal band in the cell CuA_1-CuA_2 thus forming a large (1/3 of the cell length) dark-brown rectangle; and two darker brown bands are closer to each other on the ventral hindwing than typical for the genus and flanked by paler brown bands partly separated into spots by darker veins. The lamella postvaginalis is shorter than in relatives, and has a rather straight posterior margin with a central U-shaped notch, which is about a third of the lamella length. This species is not cryptic, but because its males remain unknown and individual variation is unexplored, the most reliable identification is through DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1250.7.1:T195C, aly1250.7.1:T210C, aly276891.1.3:G129A, aly276891.1.3:T595A, aly276891.1.3:G613A, aly1675.2.10:G87G (not C), aly1675.2.

Fig. 83. *Telegonus* (*Rhabdoides*) *chuchuvianus* **sp. n.** holotype ♀ NVG-24086F12 in dorsal (left) and ventral (right) views.

10:C120C (not G), aly11945.4.1:C510C (not T), aly11945.4.1:C683C (not A), aly11945.4.1:A693A (not G); and COI barcode: T46C, C202T, A298T, A373T, T400A, T508C.

Barcode sequence of the holotype. Sample NVG-24086F12, GenBank PV550028, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACCTCTTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAACACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATAATAGGAGCCCCTGATATAGCTTTTCCACGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGTAGAATTGTAGAAAATGGTGCTGGTACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
TCACCAAGGTACATCAGTTGACCTAGCAATTTTTTCATTACATCTTGCTGGTATTTCTTCTATTCTTGGAGCCATTAACTTTATTACAACAATTATTAATATACGAATTAATAAATTATCT
TTTGATCAAATACCCTTATTTGTCTGAGCTGTAGGAATTACAGCATTATTATTATTGCTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCTGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 83 (genitalia Fig. 81e–g), bears the following five rectangular labels (1st handprinted, others printed), four white: [ECUADOR - ESM | CHUCHUVI 800 m | VI-2018], [Mark Simon Colln | MGCL Accession | # 2021-10], [DNA sample ID: | NVG-24086F12 | c/o Nick V. Grishin], [genitalia: | NVG241220-28 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Telegonus (Rhabdoides) | chuchuvianus Grishin].

Type locality. Ecuador: Esmeraldas, Chuchuví, elevation 800 m.

Etymology. The name is derived from the type locality and is an adjective.

Distribution. Currently known only from the holotype collected in northern Ecuador.

Telegonus (*Rhabdoides*) *panamus* Grishin, new species

http://zoobank.org/84351388-A1AB-48A1-82ED-169F7C16CD10

(Figs. 61 part, 84, 85a–g, 89 part)

Definition and diagnosis. Inspection of genomic trees reveals that specimens from Panama forming a clade sister to *Telegonus parmenides* (Stoll, 1781), **stat. rest.** (type locality not stated in the description, likely in Suriname) are genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 2.4% (16 bp) and, therefore, represent a new species. This new species keys (incompletely) to "*Astraptes creteus creteus*" C.14.28(d) in Evans (1952), who treated *T. parmenides* as a junior subjective synonym of *Telegonus creteus* (Cramer, 1780) (Suriname), and differs from these species by brilliantly blue (somewhat towards purple away from the wing bases in the holotype) or aquamarine (but not green) basal wing areas and body above, more restricted on the hindwing (not reaching its middle); dark ventral forewing costal area with more limited blue overscaling at the base; tornal pale area on the ventral forewing typically smaller and stronger overscaled with brown on the sides without a clearly outlined edge; a slightly narrower ampulla, and a more pointed and extended distal end of the harpe, which, as a result, is stronger concave at the dorsoposterior margin closer to its distal end (Fig. 85a, f, g). Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly535.10.1:G159A, aly535.10.1:A209G, aly2012.50.1:T78A, aly2012.50.1:A96C, aly638.4.4:C1161T; and COI barcode: T4C, C82T, T197C, T364A, T385C.

Fig. 84. *Telegonus* (*Rhabdoides*) *panamus* **sp. n.** holotype ♂ NVG-14111C10 in dorsal (left) and ventral (right) views.

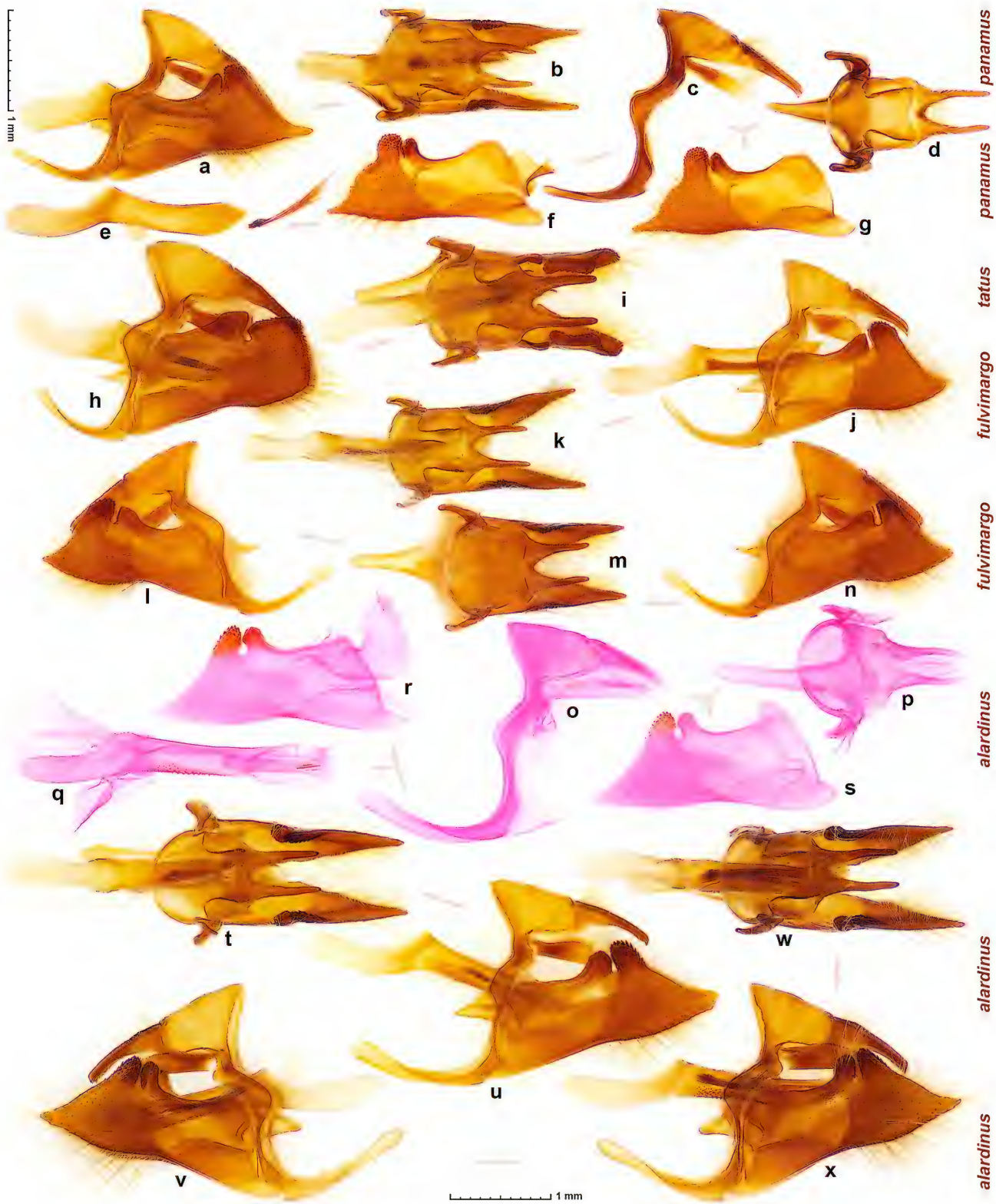


Fig. 85. Male genitalia of *Telegonus* (*Rhabdoides*) holotypes (unless indicated), data in text: **a–b)** *T. panamus* **sp. n.** NVG-14111C10; **c–g)** *T. panamus* **sp. n.** paratype NVG-23063F12; **h–i)** *T. tatus* **sp. n.** NVG-14111D05; **j–k)** *T. fulvimargo* **sp. n.** NVG-19075A12; **l–n)** *T. fulvimargo* **sp. n.** paratype NVG-24064B08; **o–s)** *T. alardinus* **sp. n.** NVG-23063G09; **t–x)** *T. alardinus* **sp. n.** paratypes: **t–u)** NVG-19075C11; **v–x)** NVG-24064B03 in different views: **a**, **c**, **e**, **h**, **j**, **n**, **o, q, u, x)** left lateral; **b**, **d**, **i**, **k**, **m**, **p**, **t**, **w)** dorsal; and **f**, **g**, **l**, **r**, **s**, **v)** right lateral: **a, b, h–n, t–x)** complete genital capsule and **c, d, o, p)** genitalia with **e, q)** aedeagus and **f, s)** right and **g, r)** left valvae detached and shown separately. Vesica is everted in **e)**, cornuti on the right. Genitalia **o–s)** were stained using Double Stain, see text. Beige arrows connect different views or parts of the same genitalia.

Barcode sequence of the holotype. Sample NVG-14111C10, GenBank PV550029, 658 base pairs:

AACCCTATATTTTATTTTTGGAATTTGAGCAGGATTAATTGGAACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCACGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGACTAGTCCCTTTAATAATAGGAGCCCCTGATATAGCTTTTCCACGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
ACATCAAGGAGCATCAGTTGACTTAGCAATTTTTTCTTTACACCTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAACTTAAATACTT
CATTTTTTGACCCAGCAGGAGGAGGAGATCCAATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 84 (genitalia Fig. 85a, b), bears the following five printed (text in italics handprinted) rectangular labels, four white: [PANAMA CANAL ZONE: | Barro Colorado Is. | *27 JULY* 1977. | Silberglied/Aiello | *AT LIGHTS*], [DNA sample ID: | NVG-14111C10 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119F02 | c/o Nick V. Grishin], [genitalia: | NVG240817-53 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | panamus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratype:** 1♂ NVG-23063F12 Panama, Panamá Province, Summit, 2-Sep-1977, R. Hesterberg leg., genitalia vial SRS-1051 (Fig. 85c–g) [MGCL].

Type locality. Panama: Panamá Oeste Province, Barro Colorado Island.

Etymology. The name is derived from the name of the country with the type locality and is treated as a masculine noun in apposition.

Distribution. Currently known only from central Panama.

Telegonus (*Rhabdoides*) *tatus* Grishin, new species

http://zoobank.org/2E3436DE-28EB-400F-9794-3865EF77ADFE

(Figs. 61 part, 85h–i, 86, 89 part)

Definition and diagnosis. A specimen from Panama (in USNM collection) that we initially identified by wing pattern as *Telegonus crana* (Evans, 1952), **stat. rest.** (type locality in Guatemala: San Gerónimo) is not in the same clade with it and instead is sister to *Telegonus cretatus* Hayward, 1939 (type locality in Ecuador: Napo), but is genetically differentiated from it at the species level (Fig. 61); e.g., their COI barcodes differ by 5.3% (35 bp), and, therefore, represents a new species. This new species keys (incompletely) to "*Astraptes alfius alfius*" C.14.27(a) in Evans (1952), which is a junior subjective synonym of *T. cretatus*, and shares unique for the genus male genitalia with a shorter and distally truncate (not pointed or rounded) harpe, but differs from it by males with even shorter and more rectangular harpe (more trapezoidal to square in *T. cretatus*), more robust ampulla (Fig. 85h); darker base of the ventral hindwing that does not strongly stand out as a paler area, bluer (rather than greener) bases of wings above, and darker ground color of the wings beneath, thus with less prominent darker bands. It differs from similar in appearance *T. crana* by the presence of a greenish-blue streak along the ventral forewing costa at the base (the base is pale-brown without blue in *T. crana*) and broader dark bands on the ventral side of wings. It differs from other relatives by a generally darker aspect reflected in the lack of a white spot in the middle of the dorsal forewing and stronger overscaled with brown area towards the costa on the ventral forewing, where the costal pale ray is separated from the central white band; and darker ventral hindwing, more weakly overscaled with yellow and broader dark bands. Due to unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1350.11.2:T175A, aly1350.11.2:A184G, aly1350.11.2:G222C, aly114.21.1:T90A, aly84.18.5:G2604A, aly6654.6.4:T384T (not C), aly671.41.1:T192T (not C), aly876.8.1: G624G (not A), aly876.8.1:A1695A (not T), aly1838.36.4:A279A (not C); and COI barcode: G389A, T400C, T406C.

Barcode sequence of the holotype. Sample NVG-14111D05, GenBank PV550030, 658 base pairs:

AACTTTATACTTTATTTTCGGAATTTGAGCAGGATTAATTGGAACTTCCTTAAGTTTACTTATTCGAACTGAATTAGGAACTCCAGGATCTTTAATTGGTGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCCCTAATAATGGGAGCCCCTGATATAGCTTTTCCACGTA
TAAATAATATAAGATTTTGACTTTTACCTCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAATATTGC
TCATCAAGGAGCATCAGTTGACTTAACAATTTTTTCCTTACACTTAGCTGGTATTTCTTCCATTTTAGGAGCTATTAACTTTATTACAACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTTGGAATTACAGCATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATCACTATACTATTAACTGATCGAAACTTAAATACCT
CATTTTTTGATCCAGCAGGAGGAGGTGATCCAATTTTATATCAACATTTATTT

Fig. 86. *Telegonus* (*Rhabdoides*) *tatus* **sp. n.** holotype ♂ NVG-14111D05 in dorsal (left) and ventral (right) views.

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 86 (genitalia Fig. 85h, i), bears the following five printed (text in italics handwritten) rectangular labels, four white: [PANAMA:PANAMA | 5 mi N El Llano | 330m 9º17'N 79º00'W | 14 Jun 1978 | leg. G.B.Small], [DNA sample ID: | NVG-14111D05 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119F03 | c/o Nick V. Grishin], [genitalia: | NVG240817-54 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | tatus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Type locality. Panama: Panamá Province, 5 mi north of El Llano, elevation 330 m, approx. GPS 9.283, −79.000.

Etymology. The name is formed from its sister species' name, *cretatus*, made shorter for this more northern relative, and is treated as a noun in apposition.

Distribution. Currently known only from the holotype collected in central Panama.

Telegonus (*Rhabdoides*) *fulvimargo* Grishin, new species

http://zoobank.org/BA7F1423-91F4-47A9-930F-F756AC10391C

(Figs. 61 part, 85j–n, 87a, 89 part)

Definition and diagnosis. Several males from southern Peru and eastern Bolivia, some identified in the USNM collection as *Telegonus meretrix* (Hewitson, 1876), **stat. rest.** (type locality in Ecuador), form a distinct clade in the genomic trees together with *T. meretrix*, not closely associated with any other species (Fig. 61). These specimens and Ecuadorian *T. meretrix* are genetically differentiated from each other at the species level in the nuclear genome (Fig. 61a, b), however, the difference in the mitochondrial genome is smaller, e.g., their COI barcodes differ by only 0.8% (5 bp). Because these specimens from Peru and Bolivia form a nuclear genome clade prominently separated from *T. meretrix*, they represent a new species. This new species keys (incompletely) to "*Astraptes chiriquensis meretrix*" C.14.30(c) in Evans (1952) and the two species share extensive brilliant-blue to aquamarine wing bases above almost reaching the discal forewing dark band, broad and nearly cross-connected dark bands on the ventral side of wings, which is overscaled with yellow, particularly in the submarginal area distad and adjacent to the outer dark band and the dark base of the costal margin on the forewing beneath (Fig. 87). However, the new species (Fig. 87a) differs from *T. meretrix* (Fig. 87b) by darker and more restricted yellow areas and overscaling on the ventral side of wings, stronger overscaled with brown and yellower marginal area more prominent than in *T. meretrix*, which has more brown scales just along the hindwing margin particularly towards the apex but stronger yellow scaling basad towards the outer dark band and more extensive yellow overscaling between the dark bands over the entire wing (i.e., the new species has a more uniformly colored submarginal plus marginal area distad of the outer dark band); a ventral hindwing postdiscal band that is stronger cut into spots by paler veins (more uniform in *T. meretrix*); the spot between veins M_1 and

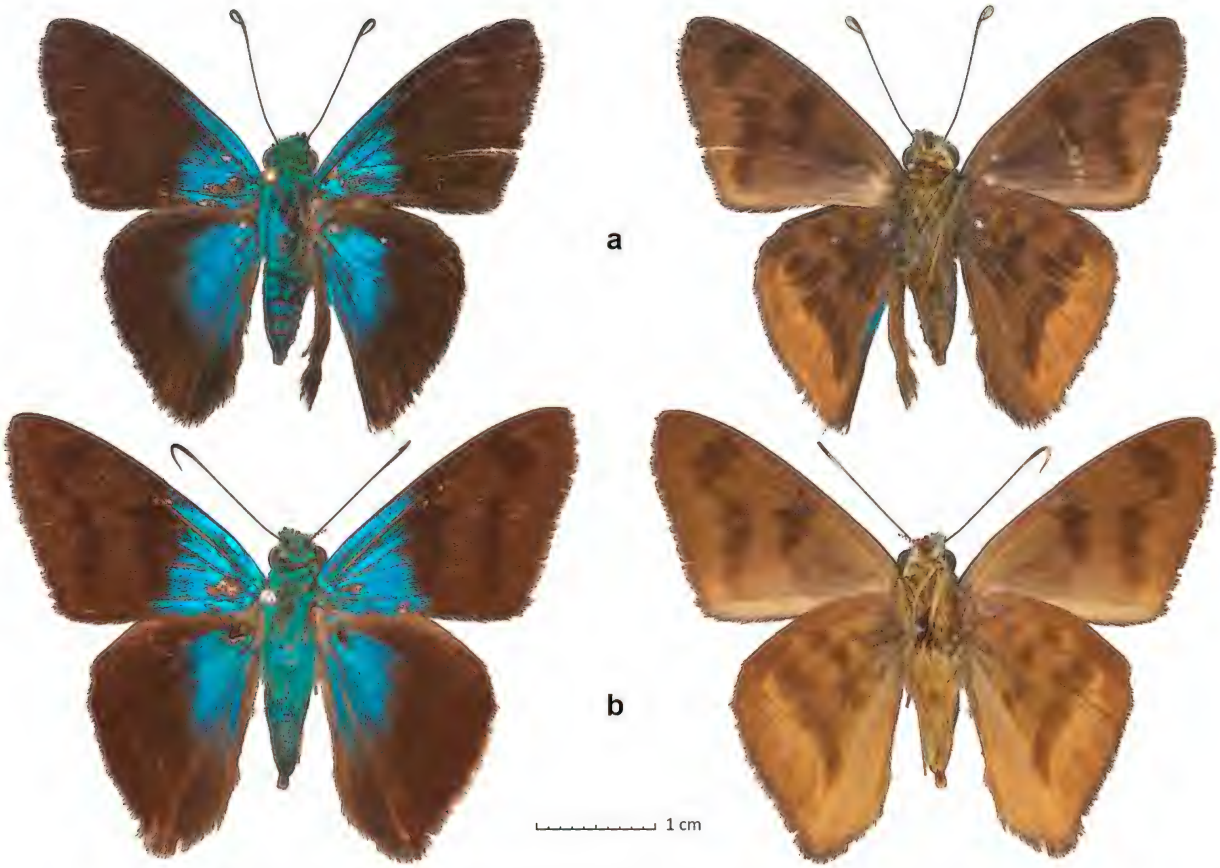


Fig. 87. Specimens of *Telegonus* (*Rhabdoides*) in dorsal (left) and ventral (right) views:
a) *T.* (*R.*) *fulvimargo* **sp. n.** holotype ♂ NVG-19075A12 Peru: Cuzco, Cosñipata Valley, 22-X-2016. S. Kinyon [USMN] and
b) *T.* (*R.*) *meretrix* non-type specimen ♂ NVG-24028D07 Ecuador: Pichincha, Santa Ines, old., R. Haensch S. [MFNB].

M_3 protruding basad from the band (closer aligned with other spots in *T. meretrix*); and typically smaller overall size. The costa of the valva is evenly convex, the ampulla nearly triangular, broader than in relatives at the base, which is slightly expanded anteriad along the costa; the ampulla is separated from the dorsal projection of the harpe by a U-shaped groove; this projection is typical for the genus in shape and size and distally is not separated from the harpe by an indentation but seamlessly curves towards the posterior end of the harpe, which is shorter than in many congeners, terminally pointed but not elongated, its dorsoposterior margin is evenly convex in lateral view without a central hump (Fig. 85j, l, n). Due to the cryptic nature of this species and poorly known individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly536.214.1:T42C, aly5745.5.8:C105G, aly5745.5.8:C111G, aly2284.23.3:G101C, aly2284.23.3:A138T; and COI barcode: T106C, C220T, A242T, T337C, A628G, T640C.

Barcode sequence of the holotype. Sample NVG-19075A12, GenBank PV550031, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAATCGGAACTTCTTTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGACGACCAAATTTATAATACT
ATTGTAACAGCTCATGCATTTATCATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATAATAGGAGCTCCTGATATAGCTTTTCCTCGTT
TAAATAATATAAGATTTTGACTTTTACCTCCATCATTAACTTTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGTACAGGATGAACAGTCTATCCCCCTCTTTCATCTAATATCGC
CCATCAAGGAACATCAGTTGATCTAGCAATTTTTTCTTTACATCTTGCAGGTATTTCTTCTATTCTTGGAGCCATTAATTTTATTACAACAATTATTAATATACGTATTAATAATTTATCT
TTTGATCAAATACCATTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATACTATTAACTGATCGAAATTTAAATACAT
CATTTTTTGACCCTGCTGGAGGGGGAGATCCAATCCTATATCAGCATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 87a (genitalia Fig. 85j, k), bears the following six printed (text in italics handwritten) rectangular labels, five white: [PERU:Cuzco 1194 m | Quebrada Santa Isabel | Cosñipata Valley *5162* | 22-X-2016 Kinyon], [DNA sample ID: | NVG-19075A12 | c/o Nick V. Grishin], [DNA sample ID: | NVG-23119F04 | c/o Nick V. Grishin], [genitalia: | NVG240817-55 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01588547], and one red [HOLOTYPE ♂ | Telegonus (Rhabdoides) | fulvimargo Grishin]. The first DNA sample (sequenced)

refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratypes:** 4♂♂ from Peru: Cuzco: 1♂ NVG-14104B02 Cosñipata Road, Quebrada Quitacalzón, elevation 1050 m, 27-Jan-2013, S. Kinyon leg. [USNM] and 1♂ NVG-24019E10 Marcapata, old, A. Seitz collection [SMF] and 1♂ NVG-18027G03, USNMENT 01465197 no detailed locality or date, old, donated by B. P. Clark, genitalia vial SRS-1837 [USNM] and 1♂ NVG-24064B08 Bolivia, La Paz Department, Sud Yungas Province, Rio Selva Resort, 2500', GPS −16.203944, −67.794139, 8-Mar-2000, T. Emmel & S. Schlachta leg., an unnumbered vial with genitalia likely dissected by D. L. Lindsley is pinned between the labels (Fig. 85l–n) [MGCL].

Type locality. Peru: Cuzco, Cosñipata Valley, Quebrada Santa Isabel, elevation 1194 m, approx. GPS −13.0333, −71.5167.

Etymology. The name is given for the fulvous (rather than "flavous") ventral hindwing marginal area and is treated as a masculine noun in apposition.

Distribution. Currently known only from the eastern slopes of the Andes in southern Peru and eastern Bolivia.

Telegonus grullus (Mabille, 1888) is a species distinct from *Telegonus latimargo* (Herrich-Schäffer, 1869)

Genomic analysis of the lectotypes of *Eudamus latimargo* Herrich-Schäffer, 1869 (type locality in tropical America to USA, sequenced as NVG-15031C08) and *Thymele grullus* Mabille, 1888 (type locality in Panama: Chiriquí, sequenced as NVG-15031B12) reveals that they belong to two distinct and not even most closely related species in different clades of the genomic trees (Fig. 61), and their COI barcodes differ by 3% (20 bp). Therefore, we propose that *Telegonus grullus* (Mabille, 1888), **stat. rest.** is a species distinct from *Telegonus latimargo* (Herrich-Schäffer, 1869). The latter species is closely related to *Telegonus alardus* (Stoll, 1790) (type locality in Surinam). Evans (1952) swapped the identities of these two species, treating *T. grullus* as a synonym of *T. alardus*, and we identify Evans's *T. latimargo* as *T. grullus*. Godman and Salvin (1893-1899), who inspected the lectotype of *T. grullus*, identified this species correctly. *Telegonus grullus* has more prominent dark spots (partly connected into bands) on the ventral forewing, darker than pure white hindwing fringes in males, and the anal fold of the hindwing is brown beneath, but the fringe near the tornus may be paler. In contrast, ventral forewing spots are "washed out" in *T. latimargo*, especially towards tornus, hindwing fringes are mostly white, and the distal part of the anal fold is white beneath. Both characters are observed in the lectotypes of these two species (Warren et al. 2024).

Telegonus fabrici Ehrmann, 1918 and *Astraptes alardus aquila* Evans, 1952 are a junior subjective synonym and a subspecies of *Telegonus latimargo* (Herrich-Schäffer, 1869), respectively

Genomic analysis of the lectotype of *Telegonus fabrici* Ehrmann, 1918 (type locality Venezuela: Caura Valley, sequenced as NVG-15096C02) currently treated as a junior subjective synonym of *Telegonus alardus alardus* (Stoll, 1790) (type locality in Suriname) is not monophyletic with it and is placed among specimens of *Telegonus latimargo* (Herrich-Schäffer, 1869) (type locality in tropical America to USA, sequenced as NVG-15031C08) (Fig. 61). Therefore, we propose that *Telegonus fabrici* Ehrmann, 1918 is a junior subjective synonym of *Telegonus latimargo* (Herrich-Schäffer, 1869), rather than of *T. alardus alardus*, resulting in a new synonym placement. Moreover, while specimens from western Colombia that we identified as *Astraptes alardus aquila* Evans, 1952 (type locality in Colombia: Cauca Valley), due to their reduced white overscaling towards the ventral hindwing margin, differ from both *T. latimargo* and *T. alardus* by this character of their wing pattern, they are genetically placed among specimens of *T. latimargo* (Fig. 61). Because subspecies are frequently defined only by their wing patterns, they do not have to be separated into clades by their overall genetic similarity. Hence, not willing to synonymize the

name, we propose to treat *A. alardus aquila* Evans, 1952 as a subspecies of *T. latimargo* forming a new species-subspecies combination: *Telegonus latimargo aquila* (Evans, 1952), **comb. nov**. Finally, both species, *T. latimargo* and *T. alardus*, are present in the Department of Tolima, Colombia (Fig. 61), although they have not been recorded at the same locality.

Telegonus (*Rhabdoides*) *alardinus* Grishin, new species

http://zoobank.org/427C08A0-E75F-4662-B454-1609D10ECC97

(Figs. 61 part, 85o–x, 88, 89 part)

Definition and diagnosis. Genomic trees reveal that specimens from Southeast and South Brazil that we identified as *Telegonus alardus alardus* (Stoll, 1790) (type locality in Suriname) formed a distinct clade genetically differentiated from other *T. alardus* populations, including *Telegonus alardus latia* (Evans, 1952) (type locality in Costa Rica) (Fig. 61): e.g., F_{st}/G_{min} of 0.22/0.014. While their COI barcodes differ from the *T. alardus* haplotype from the nominotypical populations by 0.9% (6 bp), genetic uniformity of *T. alardus* across both American continents and stronger genetic differentiation in the nuclear genome compared to that in the mitochondrial genome suggests species-level status of the Brazilian taxon. This new species keys to "*Astraptes alardus alardus*" C.14.25(c) in Evans (1952) but has the hue of brown ground color beneath more into yellow rather than red-to-purple in *T. alardus*; stronger and more contrasting with the ground color dark spotting on the ventral side basad of white margins; bluish-green areas on the dorsal side more restricted than in a typical *T. alardus*; and usually more extensive white overscaling at the ventral wing margins with a better defined inner border of white areas and white overscaling entering the apical area of the forewing. Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly12063.11.2:A48T, aly4333.9.8:C120G, aly144.42.3:T153C, aly116.28.6:G22A, aly116.28.6:A168G; and COI barcode: C136C, T220C, T418C, T508A.

Barcode sequence of the holotype. Sample NVG-23063G09, GenBank PV550032, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGATTAGTTGGAACTTCATTAAGATTACTTATTCGAACTGAATTAGGAACCCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCACGCATTTATCATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTCCCATTAATAATAGGAGCCCCCGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGACTTTTACCCCCATCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCCGGAACAGGATGAACAGTTTATCCCCCTCTTTCATCTAACATTGC
CCATCAAGGAGCATCAGTTGATTTAGCTATTTTTTCCCTACATTTAGCTGGTATCTCTTCTATTTTAGGTGCTATTAATTTTATTACTACAATTATTAATATACGAATTAATAATTTATCT
TTTGATCAAATACCTTTATTTGTATGAGCTGTAGGAATTACAGCATTATTATTATTACTTTCATTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 88 (genitalia Fig. 85o–s), bears the following five printed (text in italics handwritten) rectangular labels, four white: [BRASIL: R. de JANEIRO | Petropolis, 1500 m. | *1.V.* 197*1* | C. Callaghan], [Genit. Prep. | SRS-*831*], [A. C. Allyn | Acc. 1974-3], [DNA sample ID: | NVG-23063G09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ |

Fig. 88. *Telegonus* (*Rhabdoides*) *alardinus* **sp. n.** holotype ♂ NVG-23063G09 in dorsal (left) and ventral (right) views.

Telegonus (Rhabdoides) | alardinus Grishin]. **Paratypes:** 2♂♂ and 4♀♀ from Brazil: Rio de Janeiro: 1♂ NVG-24064B03 Magé municipality, Suruí district, km 14 of Rio–Teresópolis Highway (BR-116), 5-Jul-1971, C. Callaghan leg., genitalia NVG241111-02 (Fig. 85v–x) [MGCL], 1♀ NVG-19075D01, USNMENT 01588571 Teresópolis, Barragem Parque Nacional da Serra dos Orgãos, elevation 1100 m, approx. GPS −22.45, −43.00, 16-Feb-1995, Astrid Caldas and students leg. [USNM], and 1♀ NVG-24019B02 (no other data) old [SMF] and Santa Catarina: 1♂ NVG-19075C11 (leg DNA extraction, sequenced), NVG-23119F05 (abdomen DNA extraction and dissection), USNMENT 01588569, Joinville, Vila Nova, elevation 200 m, approx. GPS −26.367, −48.933, 23-Mar-1991, Robert K. Robbins & Olaf H. H. Mielke leg., genitalia NVG240817-56 (Fig. 85t, u) [USNM] and 1♀ NVG-24064B04 São Bento do Sul, Feb-1984, Rank leg. [MGCL] and 1♀ NVG-24028C09 Paraguay, old, P. Gladhorn S. K. [MFNB].

Type locality. Brazil: Rio de Janeiro, Petropolis, elevation 1500 m.

Etymology. The name is formed from its sister species *T. alardus* and made longer to indicate a more southern distribution of this species. The name is treated as a masculine noun in apposition.

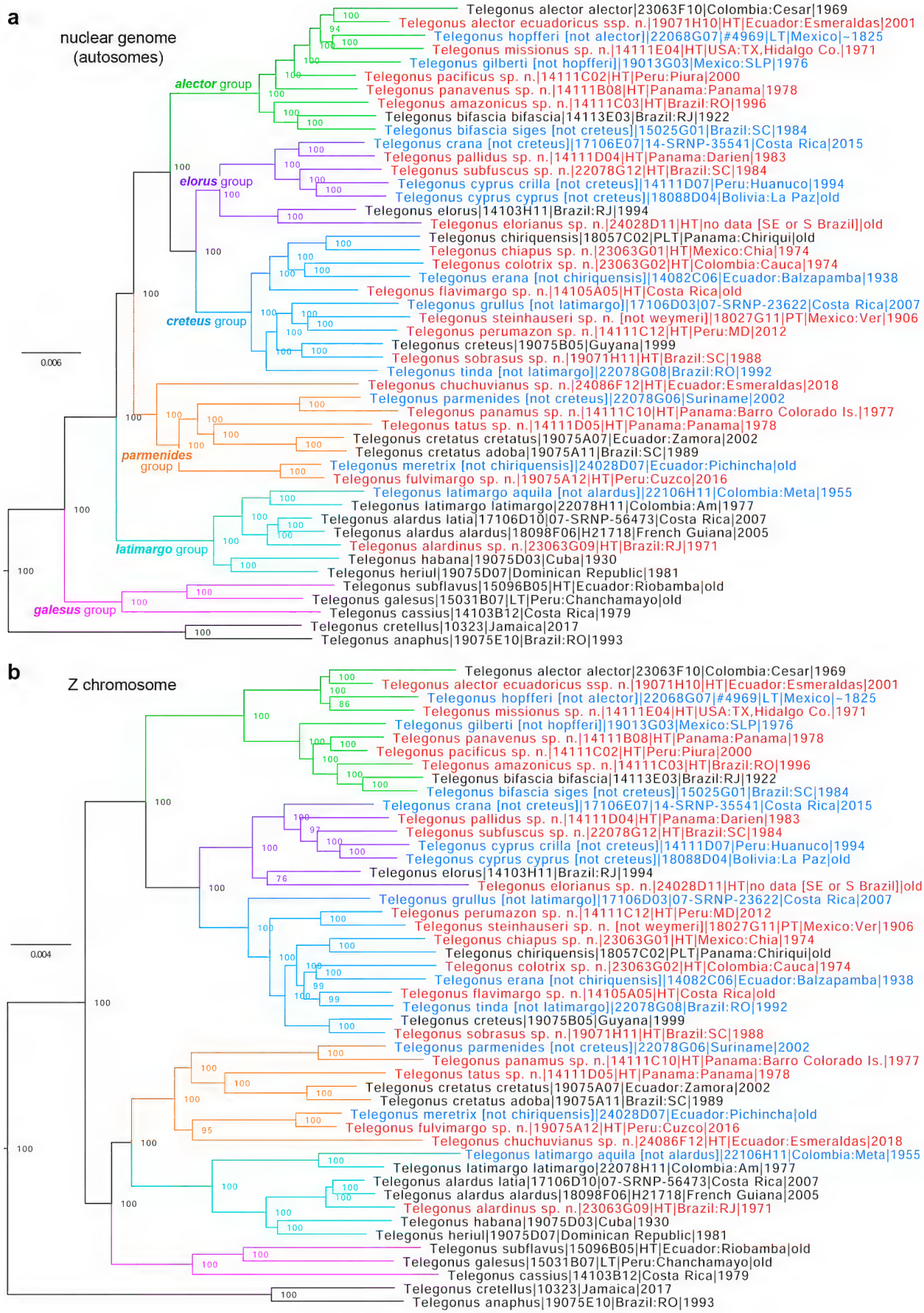
Distribution. Southeast and South Brazil and Paraguay.

Comment. Genitalia of the holotype, vial SRS-831, prepared by S. R. Steinhauser, became nearly transparent, likely due to overexposure in KOH, and were stained for photography with Double Stain containing lignin pink, acid fuchsin, GAA, lactic acid, and phenol (Fig. 85o–s).

A preliminary taxonomic list of *Telegonus* (*Rhabdoides* Scudder, 1889) species from the clade analyzed in this work

Phylogenetic trees constructed from protein-coding regions in genomic sequences reveal that the species of the subgenus *Rhabdoides* Scudder, 1889 (type species *Eudamus cellus* Boisduval & Le Conte, [1837]) in the genus *Telegonus* Hübner, [1819] (type species *Papilio talus* Cramer, 1777) from the clade (Li et al. 2019) that we analyzed in this study partition into six major subclades that we define as species groups (Fig. 89). These are all *Rhabdoides*, excluding the clades with *Telegonus anaphus* (Cramer, 1777) and *Telegonus cellus* (Boisduval & Le Conte, [1837]): *Rhabdoides* species not shown in the list below belong to the outgroup and should be placed after the last entry given in this list. We use the name of the species with the oldest valid name in each group as the group name. Although the attribution of species to these groups is the same according to the trees constructed from autosomes and the Z chromosome, the topology between and within the groups differs somewhat (compare Fig. 89a and b). Each topology is supported by confident statistics (Fig. 89), suggesting complexities in the early evolution of these species, such as incomplete lineage sorting or gene exchange. These complexities are further corroborated by the mitochondrial genome tree, which reveals a third topology differing from the nuclear tree in the placement of many species and species groups (Fig. 89).

In the list below, we attempt to order species to maximize the phenotypic similarity and geographic proximity of the list neighbors but without disrupting phylogenetic orders given in both genomic trees (Fig. 89): i.e., a strongly supported clade in the trees is a continuous segment in the list. We were guided by the following considerations. We start by ordering species groups. First, *Telegonus parmenides* (Stoll, 1781), **stat. rest.** was historically regarded as a junior subjective synonym of *Telegonus creteus* (Cramer, 1780) due to phenotypic similarity and its type locality (Suriname). However, assuming that our identification of these species is correct (see above, we follow Steinhauser's identification before designation of neotypes), these two species belong to two different species groups. Therefore, we place the *creteus* and *parmenides* species groups next to each other in the list. Second, this adjacent position of these two groups necessitates that the *elorus* group is the neighbor of the *creteus* group (on the other side from the *parmenides* group) and the *alector* species group is the neighbor of the *elorus* group (according to both trees, not to disrupt their phylogenetic order); while the *latimargo* group is the neighbor of the *parmenides* group (on the other side from the *creteus* group) and the *galesus* group is the neighbor of the *parmenides* group (according to the Z chromosome tree). These two considerations fix the order of the species groups as: *alector*, *elorus*, *creteus*, *parmenides*, *latimargo*, and *galesus*, or a


a
nuclear genome
(autosomes)
alector group
elorus group
creteus group
parmenides group
latimargo group
galesus group
0.006
Telegonus alector alector|23063F10|Colombia:Cesar|1969
Telegonus alector ecuadoricus ssp. n.|19071H10|HT|Ecuador:Esmeraldas|2001
Telegonus hopfferi [not alector]|22068G07|#4969|LT|Mexico|~1825
Telegonus missionus sp. n.|14111E04|HT|USA:TX,Hidalgo Co.|1971
Telegonus gilberti [not hopfferi]|19013G03|Mexico:SLP|1976
Telegonus pacificus sp. n.|14111C02|HT|Peru:Piura|2000
Telegonus panavenus sp. n.|14111B08|HT|Panama:Panama|1978
Telegonus amazonicus sp. n.|14111C03|HT|Brazil:RO|1996
Telegonus bifascia bifascia|14113E03|Brazil:RJ|1922
Telegonus bifascia siges [not creteus]|15025G01|Brazil:SC|1984
Telegonus crana [not creteus]|17106E07|14-SRNP-35541|Costa Rica|2015
Telegonus pallidus sp. n.|14111D04|HT|Panama:Darien|1983
Telegonus subfuscus sp. n.|22078G12|HT|Brazil:SC|1984
Telegonus cyprus crilla [not creteus]|14111D07|Peru:Huanuco|1994
Telegonus cyprus cyprus [not creteus]|18088D04|Bolivia:La Paz|old
Telegonus elorus|14103H11|Brazil:RJ|1994
Telegonus elorianus sp. n.|24028D11|HT|no data [SE or S Brazil]|old
Telegonus chiriquensis|18057C02|PLT|Panama:Chiriqui|old
Telegonus chiapus sp. n.|23063G01|HT|Mexico:Chia|1974
Telegonus colotrix sp. n.|23063G02|HT|Colombia:Cauca|1974
Telegonus erana [not chiriquensis]|14082C06|Ecuador:Balzapamba|1938
Telegonus flavimargo sp. n.|14105A05|HT|Costa Rica|old
Telegonus grullus [not latimargo]|17106D03|07-SRNP-23622|Costa Rica|2007
Telegonus steinhauseri sp. n. [not weymeri]|18027G11|PT|Mexico:Ver|1906
Telegonus perumazon sp. n.|14111C12|HT|Peru:MD|2012
Telegonus creteus|19075B05|Guyana|1999
Telegonus sobrasus sp. n.|19071H11|HT|Brazil:SC|1988
Telegonus tinda [not latimargo]|22078G08|Brazil:RO|1992
Telegonus chuchuvianus sp. n.|24086F12|HT|Ecuador:Esmeraldas|2018
Telegonus parmenides [not creteus]|22078G06|Suriname|2002
Telegonus panamus sp. n.|14111C10|HT|Panama:Barro Colorado Is.|1977
Telegonus tatus sp. n.|14111D05|HT|Panama:Panama|1978
Telegonus cretatus cretatus|19075A07|Ecuador:Zamora|2002
Telegonus cretatus adoba|19075A11|Brazil:SC|1989
Telegonus meretrix [not chiriquensis]|24028D07|Ecuador:Pichincha|old
Telegonus fulvimargo sp. n.|19075A12|HT|Peru:Cuzco|2016
Telegonus latimargo aquila [not alardus]|22106H11|Colombia:Meta|1955
Telegonus latimargo latimargo|22078H11|Colombia:Am|1977
Telegonus alardus latia|17106D10|07-SRNP-56473|Costa Rica|2007
Telegonus alardus alardus|18098F06|H21718|French Guiana|2005
Telegonus alardinus sp. n.|23063G09|HT|Brazil:RJ|1971
Telegonus habana|19075D03|Cuba|1930
Telegonus heriul|19075D07|Dominican Republic|1981
Telegonus subflavus|15096B05|HT|Ecuador:Riobamba|old
Telegonus galesus|15031B07|LT|Peru:Chanchamayo|old
Telegonus cassius|14103B12|Costa Rica|1979
Telegonus cretellus|10323|Jamaica|2017
Telegonus anaphus|19075E10|Brazil:RO|1993
b
Z chromosome
0.004
Telegonus alector alector|23063F10|Colombia:Cesar|1969
Telegonus alector ecuadoricus ssp. n.|19071H10|HT|Ecuador:Esmeraldas|2001
Telegonus hopfferi [not alector]|22068G07|#4969|LT|Mexico|~1825
Telegonus missionus sp. n.|14111E04|HT|USA:TX,Hidalgo Co.|1971
Telegonus gilberti [not hopfferi]|19013G03|Mexico:SLP|1976
Telegonus panavenus sp. n.|14111B08|HT|Panama:Panama|1978
Telegonus pacificus sp. n.|14111C02|HT|Peru:Piura|2000
Telegonus amazonicus sp. n.|14111C03|HT|Brazil:RO|1996
Telegonus bifascia bifascia|14113E03|Brazil:RJ|1922
Telegonus bifascia siges [not creteus]|15025G01|Brazil:SC|1984
Telegonus crana [not creteus]|17106E07|14-SRNP-35541|Costa Rica|2015
Telegonus pallidus sp. n.|14111D04|HT|Panama:Darien|1983
Telegonus subfuscus sp. n.|22078G12|HT|Brazil:SC|1984
Telegonus cyprus crilla [not creteus]|14111D07|Peru:Huanuco|1994
Telegonus cyprus cyprus [not creteus]|18088D04|Bolivia:La Paz|old
Telegonus elorus|14103H11|Brazil:RJ|1994
Telegonus elorianus sp. n.|24028D11|HT|no data [SE or S Brazil]|old
Telegonus grullus [not latimargo]|17106D03|07-SRNP-23622|Costa Rica|2007
Telegonus perumazon sp. n.|14111C12|HT|Peru:MD|2012
Telegonus steinhauseri sp. n. [not weymeri]|18027G11|PT|Mexico:Ver|1906
Telegonus chiapus sp. n.|23063G01|HT|Mexico:Chia|1974
Telegonus chiriquensis|18057C02|PLT|Panama:Chiriqui|old
Telegonus colotrix sp. n.|23063G02|HT|Colombia:Cauca|1974
Telegonus erana [not chiriquensis]|14082C06|Ecuador:Balzapamba|1938
Telegonus flavimargo sp. n.|14105A05|HT|Costa Rica|old
Telegonus tinda [not latimargo]|22078G08|Brazil:RO|1992
Telegonus creteus|19075B05|Guyana|1999
Telegonus sobrasus sp. n.|19071H11|HT|Brazil:SC|1988
Telegonus parmenides [not creteus]|22078G06|Suriname|2002
Telegonus panamus sp. n.|14111C10|HT|Panama:Barro Colorado Is.|1977
Telegonus tatus sp. n.|14111D05|HT|Panama:Panama|1978
Telegonus cretatus cretatus|19075A07|Ecuador:Zamora|2002
Telegonus cretatus adoba|19075A11|Brazil:SC|1989
Telegonus meretrix [not chiriquensis]|24028D07|Ecuador:Pichincha|old
Telegonus fulvimargo sp. n.|19075A12|HT|Peru:Cuzco|2016
Telegonus chuchuvianus sp. n.|24086F12|HT|Ecuador:Esmeraldas|2018
Telegonus latimargo aquila [not alardus]|22106H11|Colombia:Meta|1955
Telegonus latimargo latimargo|22078H11|Colombia:Am|1977
Telegonus alardus latia|17106D10|07-SRNP-56473|Costa Rica|2007
Telegonus alardus alardus|18098F06|H21718|French Guiana|2005
Telegonus alardinus sp. n.|23063G09|HT|Brazil:RJ|1971
Telegonus habana|19075D03|Cuba|1930
Telegonus heriul|19075D07|Dominican Republic|1981
Telegonus subflavus|15096B05|HT|Ecuador:Riobamba|old
Telegonus galesus|15031B07|LT|Peru:Chanchamayo|old
Telegonus cassius|14103B12|Costa Rica|1979
Telegonus cretellus|10323|Jamaica|2017
Telegonus anaphus|19075E10|Brazil:RO|1993

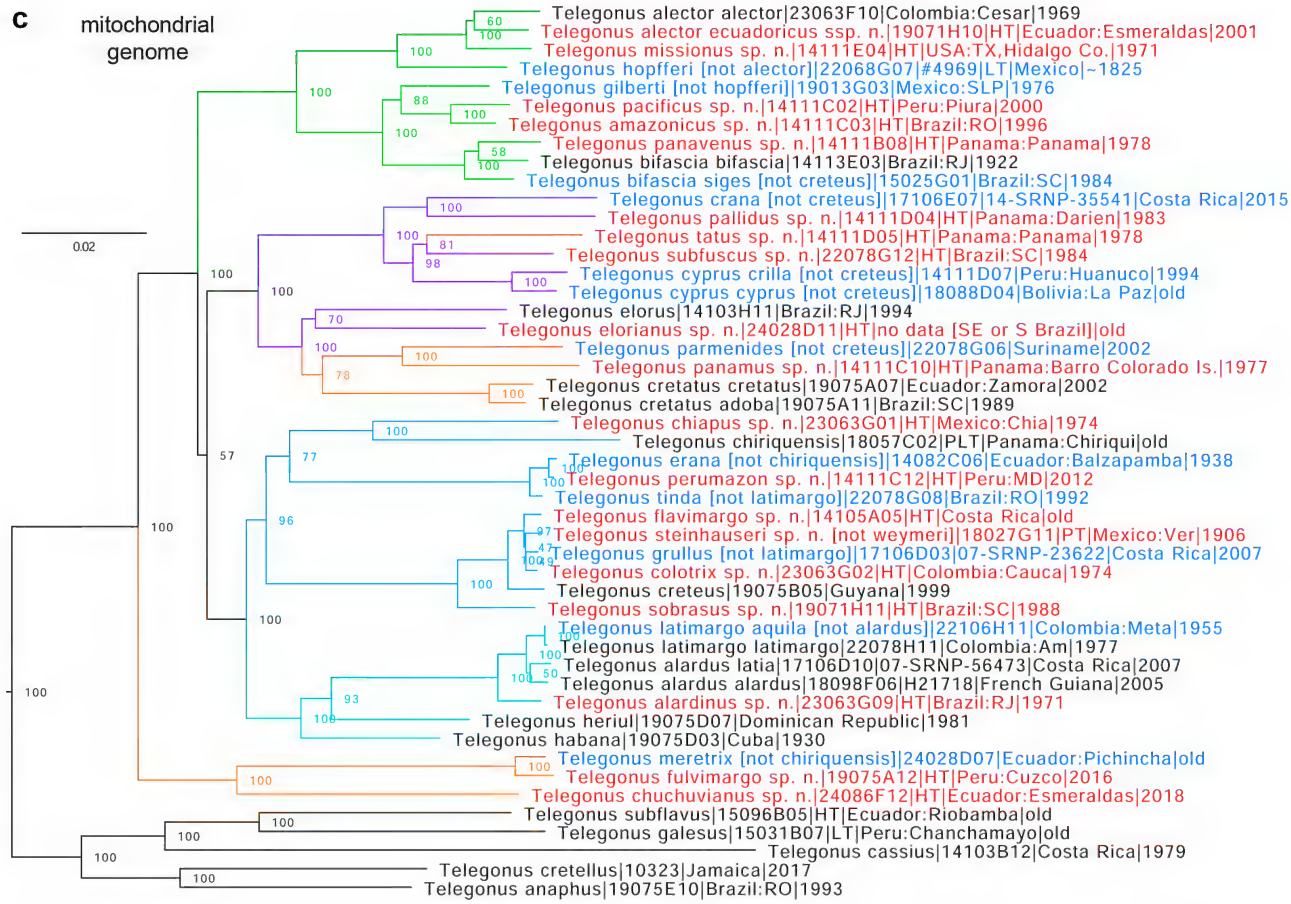


Fig. 89. Phylogenetic trees of *Telegonus* species analyzed in this study inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 9,184,581 positions, **b)** the Z chromosome, based on 319,194 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species groups are colored differently: *alector* group (green), *elorus* group (purple), *creteus* group (blue), *parmenides* group (orange), *latimargo* group (cyan), and *galesus* group (magenta). New taxa proposed in this work are labeled in red, and those with taxonomic changes, such as subspecies-to-species or synonym-to-species status or transfer of a subspecies between species (changes indicated in brackets) are labeled in blue.

reverse of this order. Third, we choose to start the list from the *alector* group because of the phenotypic similarity between *Telegonus alector* (C. Felder & R. Felder, 1867) and the *Telegonus fulgerator* (Walch, 1775) group (basal area of ventral hindwing by the costa is white and forewings are with a central pale band at least in some species), the latter being placed in the list before the species analyzed in this work.

We use similar considerations to order species within each species group. When the order is inconsistent between the autosome and the Z chromosome trees, we select the Z chromosome order. Phylogenetic trees constructed from genes encoded in the Z chromosome typically correlate better with species trees due to less introgression and gene exchange involving the Z chromosome. One challenge that we met was the presence of both yellow-margined (e.g., *T. chiriquensis* vs. *T. fulvimargo* **sp. n.**: both species have extensive yellow scaling in the submarginal area of the ventral hindwing, giving an appearance of a marginal yellow band) and brown-margined (e.g., *T. creteus* vs. *T. parmenides*: both species possess mostly brown margins) species in the *creteus* and *parmenides* groups. Because it is not possible to satisfy placing both wing pattern categories next to each other in the list without violating phylogenetic constraints, only one of them must be chosen. We chose to place brown-margined species (*T. creteus* and *T. parmenides* with their closest relatives) adjacent in the list, thus placing the *creteus* and the *parmenides* groups near each other due to the similarity between them and the resulting confusion in the literature about these species. Consequently, the yellow-margined species ended up on opposite sides of their corresponding groups. Compensating for this by adjusting the order of species in other groups, we

made these yellow-margined species adjacent to pale- or yellow-margined species in species groups that are closest to them in the list (the *elorus* group is adjacent to the *creteus* group, and the *latimargo* group is next to the *parmenides* group). We note that any phylogenetic arrangement precludes placing all pale-margined species together in the list, because they are distributed among four species groups, three of which include brown-margined species. Moreover, one species (*T. weymeri*) is variable in the expression of yellow submarginal overscaling, and its sister species (*T. perumazon* **sp. n.**) is brown-margined. Further refinements of the list order are encouraged.

In the resulting arrangement below, species of *Rhabdoides* excluding the clades with *Telegonus anaphus* (Cramer, 1777) and *Telegonus cellus* (Boisduval & Le Conte, [1837] are given. The list also includes species discovered by Steinhauser (1987) ("four new species will be added to the group") that fall within these species groups but remain unpublished, shown in gray font. Type localities (general area only: state, region, department, or county) are in gray font. New taxa described in this study and the category of taxonomic change are in red font. Taxonomic treatment before this work (for valid names) or the category of synonym (for synonyms) and comments are shown in smaller font following a vertical bar | after the type locality; an equal sign = precedes synonyms given in their original genus combination; and a double dagger ‡ marks unavailable names. The list covers 50 valid taxa comprising 44 species (18 newly proposed here and 4 yet undescribed) and 6 additional subspecies (1 new): i.e., 27 previously known and 23 undescribed before this work. Our study follows the trend to reveal approximately as many new Hesperiidae taxa as previously described ones in nearly every genus under revision (Austin and Mielke 1998; Austin and Mielke 2008; Medeiros et al. 2019; Siewert et al. 2020).

Genus ***Telegonus*** Hübner, [1819]: type species *Papilio talus* Cramer, 1777

Subgenus *Rhabdoides* Scudder, 1889: type species *Eudamus cellus* Boisduval & Le Conte, [1837]

alector species group

Telegonus alector (C. Felder & R. Felder, 1867)

Telegonus alector alector (C. Felder & R. Felder, 1867): Colombia: Bogota

Telegonus alector ecuadoricus Grishin, **ssp. n.**; Ecuador: Esmeraldas

Telegonus hopfferi (Plötz, 1881), **stat. rest.**; Mexico [likely C or S Mexico] | was a subspecies of *alector*

= *Thracides uridon* Dyar, 1912: Mexico: Guerrero

Telegonus missionus Grishin, **sp. n.**; USA: Texas, Hidalgo Co.

Telegonus gilberti (Freeman, 1969), **stat. rest.**; Mexico: San Luis Potosí | was a synonym of *hopfferi*

Telegonus panavenus Grishin, **sp. n.**; Panama: Panamá

Telegonus pacificus Grishin, **sp. n.**; Peru: Piura

Telegonus amazonicus Grishin, **sp. n.**; Brazil: Rondônia

Telegonus bifascia (Herrich-Schäffer, 1869): likely Brazil

Telegonus bifascia bifascia (Herrich-Schäffer, 1869): likely Brazil

Telegonus bifascia siges Mabille, 1903, **comb. nov.**; Brazil [likely S] | was a subspecies of *creteus*

elorus species group

Telegonus crana (Evans, 1952), **stat. rest.**; Guatemala: San Gerónimo | was a subspecies of *creteus*

= *Astraptes escalantei* Freeman, 1967; Mexico: Chiapas | junior subjective synonym

Telegonus pallidus Grishin, **sp. n.**; Panama: Darién

Telegonus sp. undescribed # 1, Steinhauser MS.: S. America

Telegonus subfuscus Grishin, **sp. n.**; Brazil: Santa Catarina

Telegonus cyprus (Evans, 1952), **stat. rest.** | was a subspecies of *creteus*

Telegonus cyprus crilla (Evans, 1952), **new ssp. placement**: Ecuador: Zamora

Telegonus cyprus cyprus (Evans, 1952): Bolivia: Yungas & La Paz

Telegonus elorus (Hewitson, 1867): no data [likely SE or S Brazil]

= *Eudamus blasius* Plötz, 1881; "Cuba" [likely SE or S Brazil] | junior subjective synonym

= *Telegonus pheres* Mabille, 1903; Brazil: Santa Catarina | junior subjective synonym

= *Telegonus subblasius* Strand, 1921; Argentina: Misiones | junior subjective synonym

Telegonus elorianus Grishin, **sp. n.**: unknown, likely SE or S Brazil

creteus species group

Telegonus grullus (Mabille, 1888), **stat. rest.**: Panama: Chiriquí | was a synonym of *latimargo*

Telegonus sp. undescribed #2, Steinhauser MS.: Brazil

Telegonus perumazon Grishin, **sp. n.**: Peru: Madre de Dios

Telegonus steinhauseri Grishin, **sp. n.**: Mexico: Veracruz

=‡ *Telegonus chiriquensis* form *godmani* Williams, 1927: Mexico (Tab) and Nicaragua | infrasubspecific

Telegonus chiapus Grishin, **sp. n.**: Mexico: Chiapas

Telegonus chiriquensis Staudinger, 1875: Panama: Chiriquí

= *Aethilla weymeri* Plötz, 1882: ? [Panama] | junior subjective synonym

Telegonus colotrix Grishin, **sp. n.**: Colombia: Cauca

Telegonus erana (Evans, 1952), **stat. nov.**: Ecuador: Balzapamba | was a subspecies of *chiriquensis*

Telegonus sp. undescribed #3, Steinhauser MS.: Bolivia

Telegonus sp. undescribed #4, Steinhauser MS.: Panama

Telegonus flavimargo Grishin, **sp. n.**: Costa Rica: Limón

Telegonus tinda (Evans, 1952), stat. conf.: Brazil: Pará | Evans (1952) treated it as a subspecies of *latimargo*

Telegonus creteus (Cramer, 1780): Suriname

Telegonus sobrasus Grishin, **sp. n.**: Brazil: Santa Catarina

parmenides species group

Telegonus chuchuvianus Grishin, **sp. n.**: Ecuador: Esmeraldas

Telegonus parmenides (Stoll, 1781), **stat. rest.**: likely Suriname | was a synonym of *creteus*

Telegonus panamus Grishin, **sp. n.**: Panama: Barro Colorado Island

Telegonus tatus Grishin, **sp. n.**: Panama: Panamá

Telegonus cretatus Hayward, 1939

Telegonus cretatus cretatus Hayward, 1939: Ecuador: Napo

= *Astraptes alfius alfius* Evans, 1952: Brazil: Amazonas | junior subjective synonym

Telegonus cretatus adoba (Evans, 1952): Brazil: Espirito Santo

Telegonus meretrix (Hewitson, 1876), **stat. rest.**: Ecuador | was a subspecies of *chiriquensis*

Telegonus fulvimargo Grishin, **sp. n.**: Peru: Cuzco

latimargo species group

Telegonus latimargo (Herrich-Schäffer, 1869)

Telegonus latimargo aquila (Evans, 1952), **comb. n.**: Colombia: Valle | was a subspecies of *alardus*

Telegonus latimargo latimargo (Herrich-Schäffer, 1869): Tropical America to USA

=‡ *Telegonus cartomes* Mabille & Boullet, 1912: no data | nomen nudum (proposed in synonymy)

= *Telegonus fabrici* Ehrmann, 1918: Venezuela: Caura Valley | junior subjective synonym (was of *alardus*)

Telegonus alardus (Stoll, 1790)

Telegonus alardus latia (Evans, 1952): Costa Rica

Telegonus alardus alardus (Stoll, 1790): Suriname

Telegonus alardinus Grishin, **sp. n.**: Brazil: Rio de Janeiro

Telegonus habana (Lucas, 1857): Cuba

Telegonus heriul Mabille & Boullet, 1912: "Brazil" [Dominican Republic]

= *Telegonus antiquus* Skinner, 1920: Dominican Republic | junior subjective synonym

= *Telegonus domingensis* Joicey & Talbot, 1924: Dominican Republic | junior subjective synonym

galesus species group

Telegonus subflavus Grishin, 2022: Ecuador: Chimborazo

=‡ *Telegonus galesus* form *subflavus* Williams, 1927: Ecuador: Chimborazo | infrasubspecific name

Telegonus galesus Mabille, 1888: Peru: Chanchamayo

Telegonus cassius (Evans, 1952): Costa Rica: Irazú

We regard *Eudamus oenander* Hewitson, 1876 (type locality in Brazil: Pará) as a junior subjective synonym of *Aroma aroma* (Hewitson, 1867) (type locality in Brazil: Pará) in the subfamily Hesperiinae Latreille, 1809 (pending search for it syntypes or neotype designation) and do not include this name in the list because it does not belong to *Telegonus* (*Rhabdoides*). Evans (1952) treated this taxon as "*Astraptes chiriquensis oenander*" thus considering it to be related to the species in the above list.

Subfamily Pyrginae Burmeister, 1878
Tribe Carcharodini Verity, 1940

Pellicia (*Hemipteris*) *meno* (Mabille, 1889) is a valid species distinct from *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870

Genomic sequencing of the holotype of *Arteurotia meno* Mabille, 1889 (type locality in Panama, sequenced as NVG-15032E05), currently a subspecies of *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870 (type locality in Mexico and La Guaira, [Venezuela], a syntype from Venezuela sequenced as NVG-15032E10), reveals that it is not monophyletic with it and instead belongs to the subgenus *Hemipteris* Mabille, 1889 (type species *Hemipteris fumida* Mabille, 1889, currently treated as a junior subjective synonym of *Pellicia tyana* Plötz, 1882, but see below) (Fig. 90). Because *A. meno* is not conspecific with any older name in this subgenus, we propose that *Pellicia* (*Hemipteris*) *meno* (Mabille, 1889), **stat. rest.** is a valid species distinct from *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870.

Pellicia brasiliensis R. Williams & E. Bell, 1939 is a subspecies of *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870

Genomic analysis of the holotype of *Pellicia brasiliensis* R. Williams & E. Bell, 1939 (type locality in Brazil: Minas Gerais, sequenced as NVG-15097B10), currently a junior subjective synonym of *Pellicia* (*Hemipteris*) *meno* (Mabille, 1889), **stat. rest.** (type locality in Panama, holotype sequenced as NVG-15032E05) reveals that it is not monophyletic with it, but instead groups closely with *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870 (type locality in Mexico and La Guaira, [Venezuela]) (Fig. 90). The current synonymy follows Evans (1953), who likely misidentified *P. meno* and mistook *P. brasiliensis* for it. Therefore, we propose that *Pellicia* (*Pellicia*) *dimidiata brasiliensis* R. Williams & E. Bell, 1939, **stat. nov.** is a valid subspecies.

Pellicia (*Hemipteris*) *zamia* (Plötz, 1882) is a valid species distinct from *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870

Genomic sequencing of a syntype of *Pellicia zamia* Plötz, 1882 (type locality in South America, sequenced as NVG-15032E08), currently a subspecies of *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870 (type locality in Mexico and La Guaira, [Venezuela], a syntype from Venezuela sequenced as NVG-15032E10), reveals that it is not monophyletic with it and instead belongs to the subgenus *Hemipteris* Mabille, 1889 (type species *Hemipteris fumida* Mabille, 1889, currently treated as a junior subjective synonym of *Pellicia tyana* Plötz, 1882, but see below) and is closely related to *Pellicia* (*Hemipteris*) *meno* (Mabille, 1889), **stat. rest.** (type locality in Panama, holotype sequenced as NVG-15032E05) (Fig. 90). Because *P. zamia* is not conspecific with any older name in this subgenus, we propose that *Pellicia* (*Hemipteris*) *zamia* Plötz, 1882, **stat. rest.** is a valid species distinct from *Pellicia* (*Pellicia*) *dimidiata* Herrich-Schäffer, 1870. We hypothesize that Evans (1953) placed *P. zamia* as a subspecies of *P. dimidiata* because he misidentified *P. zamia*, and the specimens he identified as "*P. zamia*" are probably *Pellicia theon* Plötz, 1882 (type locality in South America, lectotype sequenced as NVG-15032E09 and shown in Fig. 91a and Godman's (1907) copy of the original Plötz's drawing t. 200 in Fig. 91b), which he misidentified as well, and the specimens he identified as "*P. theon*" may be, at least in part, *Pellicia nema* Williams and Bell, 1939 (type locality in Brazil: Mato Grosso, holotype sequenced as NVG-15097B11).

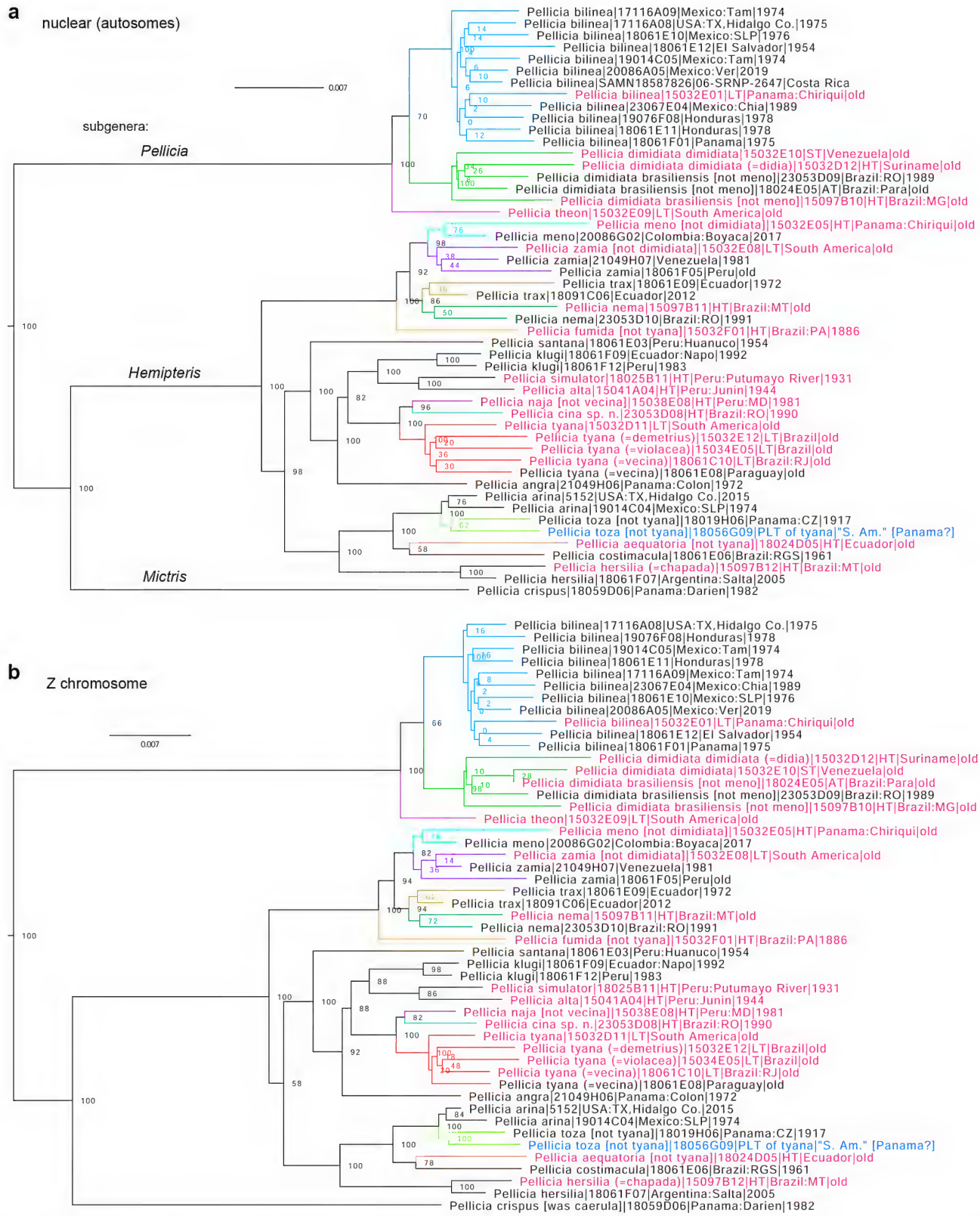
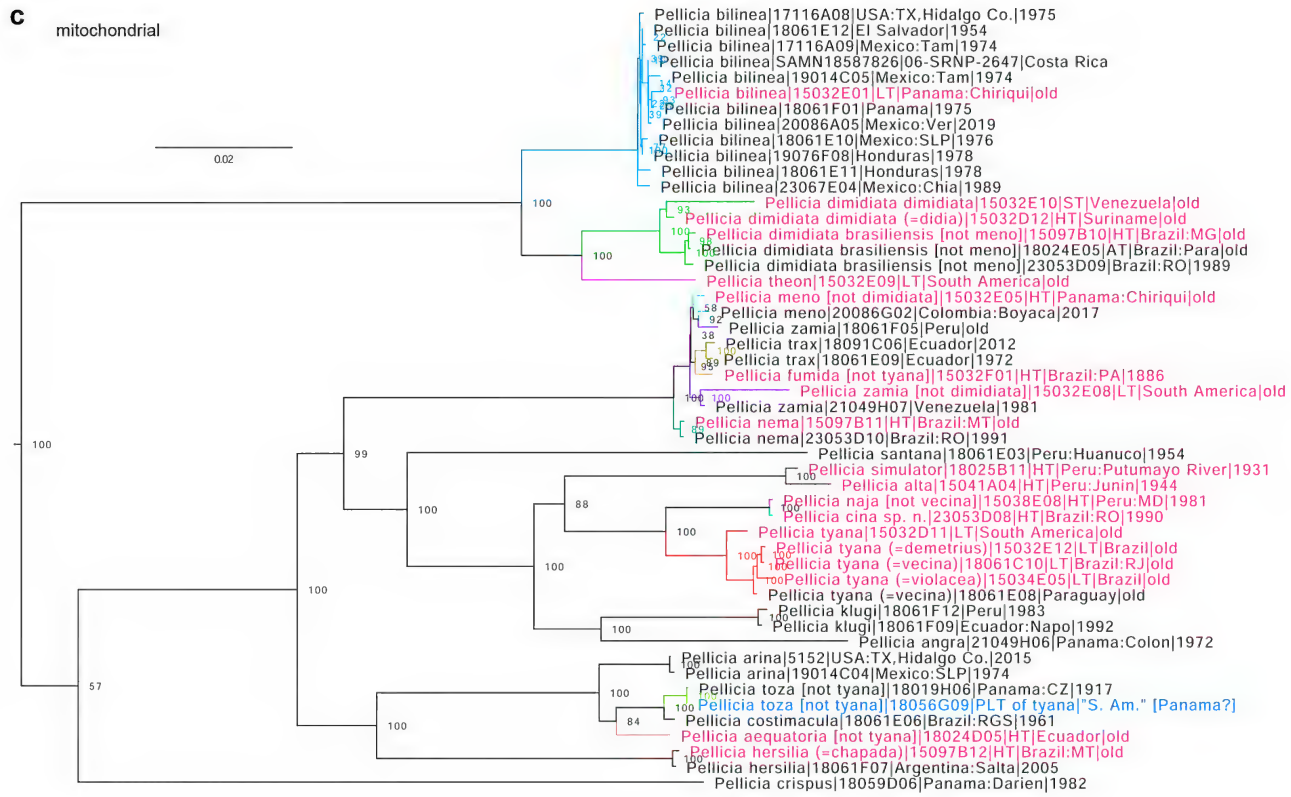


Fig. 90. Phylogenetic trees of selected *Pellicia* species inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** [see next page] the mitochondrial genome. Primary type specimens are labeled in red-purple, and a paralectotype of *P. tyana* (not conspecific with the lectotype) is labeled in blue. Different species mentioned in the text are shown in different colors. The sequence of SAMN18587826 is taken from the alignment provided in Kawahara et al. (2023).



In the light of all these misidentifications, to stabilize nomenclature and define the name *P. zamia* objectively, N.V.G. hereby designates the sequenced syntype in the MFNB collection that is shown in Fig. 91c, is similar to Godman's (1907) copy of Plötz's original drawing t. 201 (Fig. 91d), and bears the following nine labels (1st red, others white; 3rd to 7th handwritten, others printed): [typus], [Coll. Weymer], [Pellicia (156d) | Zamia Pl.], [H S | 46 | Weymer], [52 | Weymer], [26:16.], [Zamia Plötz il. | Amer.mer.], [{QR Code} http://coll.mfn-berlin.de/u/ | 940b9c], [DNA sample ID: | NVG-15032E08 | c/o Nick V. Grishin] as the **lectotype** of *Pellicia zamia* Plötz, 1882. Handwriting on the 2nd and 7th labels matches that of Plötz and Weymer, respectively. The label [26:16.] corresponds to the number for *P. zamia* in Mabille's catalog (1903). The mitochondrial genome of the lectotype is very similar to that of a specimen from Venezuela. Therefore, we suggest that the type locality of *P. zamia* may have been in Venezuela, but sequencing of additional specimens across the range is needed to support this more convincingly. The lectotype is missing its abdomen, and its right hindwing is torn from the outer margin near the costa almost to the base. Images of this specimen (Fig. 91c) photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15032E08, GenBank PV550033, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCAGGAATAGTAGGAACATCCTTAAGTTTACTTATTCGATCTGAATTAGGTACTCCTGGTTCTTTAATTGGAGATGATCAAATTTATAACACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATCATAATTGGTGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCTCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCTTTAACTTTATTAATTTCAAGAAGTATTGTAGAAAATGGTGCTGGAACTGGTTGAACTGTTTATCCTCCTTTATCAGCTAATATTGC
CCATCAAGGATCCTCTGTTGATTTAGCAATTTTTTCATTACATTTAGCAGGTATTTCCTCTATTTTAGGTGCTATTAATTTTATTACAACTATTATCAATATACGAGTTAATAATTTATTA
TTTGATCAAATGCCTTTATTTGTTTGAGCAGTAGGAATTACAGCTTTACTTTTATTATTATCATTACCAGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAATACAT
CTTTTTTCGACCCTGCAGGAGGCGGAGATCCAATTTTATATCAACATTTATTC

Lectotype designations for *Pellicia tyana* Plötz, 1882, *Arteurotia demetrius* Plötz, 1882, *Pellicia violacea* Mabille, 1891, and *Pellicia vecina* Schaus, 1902

Genomic analysis of primary type specimens of *Pellicia* Herrich-Schäffer, 1870 (type species *Pellicia dimidiata* Herrich-Schäffer, 1870) reveals many inconsistencies with the current classification (Mielke 2005). Here, we stabilize nomenclature with lectotype designations. We encountered two problems with

the syntypes of the four taxa discussed here. First, we found two credible syntypes of *Pellicia tyana* Plötz, 1882 (type locality in South America), and the syntype in MFNB (NVG-15032D11, Figs. 90, 91g) is not conspecific with the syntype in ZSMC (NVG-18056G09, Figs. 90, 91e, f). Both syntypes bear identification labels written by Plötz. Additionally, the ZSMC syntype bears a red label with the first line

Fig. 91. Type specimens and illustrations of *Pellicia* species described by Plötz, data in text: **a)** *P. theon* lectotype NVG-15032E09; **b)** *P. theon* drawing t. 200; **c)** *P. zamia* lectotype NVG-15032E08; **d)** *P. zamia* drawing t. 201; **e)** *P. toza* **stat. nov.** specimen NVG-18056G09, which is a non-conspecific paralectotype of *P. tyana*, with its labels shown in **f)** and reduced by a quarter compared to specimens with the scale shown on the right; **g)** *P. tyana* lectotype NVG-15032D11; **h)** *P. tyana* drawing t. 202; **i)** *Arteurotia demetrius* **syn. nov.** of *P. tyana*, NVG-15032E12; **j)** *A. demetrius* drawing t. 205. The drawings are Godman's copies of Plötz's original illustrations (likely drawn by Horace Knight) (Godman 1907) and are in BMNH. Images b), d), h), and j) are © of the Trustees of the Natural History Museum London and are made available under Creative Commons License 4.0 (https:// creativecommons.org/licenses/by/4.0/).

"Lectotypus" but the designation remains unpublished. However, the MFNB syntype (sequenced as NVG-15032D11) agrees better with the original description and Godman's (1907) copies (in BMNH and USNM) of unpublished Plötz's drawing t[afel]. 202 of *P. tyana* (Fig. 91h): it has more uniform violaceous overscaling towards the tornus of the ventral hindwing (as the drawing and description: "underside … hindwing lilac-gray in the posterior half" (Plötz 1882b)) vs. violaceous overscaling in the ZSMC syntype having an appearance of two crossbands in the posterior part of the wing (discal and postdiscal) plus violaceous overscaling along the outer margin. Moreover, the MFNB syntype is indeed from South America, as deduced from genomic sequencing, but the ZSMC syntype is likely to be from Panama, although it bears a label "S America". A similar locality label is on a ZSMC syntype of *Staphylus vincula* (Plötz, 1886) (type locality in Panama), which was also not from South America, based on genomic comparison (Zhang et al. 2022d). Therefore, we conclude that the syntype in MFNB represents Plötz's concept of *P. tyana* better than the ZSMC syntype.

To stabilize nomenclature and define the name *P. tyana* objectively, N.V.G. hereby designates a syntype in the MFNB collection that is shown in Fig. 91g and bears the following ten labels (1st red, others white; 3rd to 8th handwritten, others printed): [typus], [Coll. Weymer], [Tyana Pltz | taf 202.], [Pellicia (156♀) | Plana Pl.], [H S | 72 | Weymer], [54 | Weymer], [26:15.], [Tyana Plötz i l. | Plana Plötz il. | (olim) |Amer.mer.], [{QR Code} http://coll.mfn-berlin.de/u/ | 940b8d], [DNA sample ID: | NVG-15032D11 | c/o Nick V. Grishin] as the **lectotype** of *Pellicia tyana* Plötz, 1882. Handwriting on the 3rd and 8th labels matches that of Weymer, and on the 4th that of Plötz, and taf[el] 202 is the number of the unpublished Plötz's drawing of *P. tyana* mentioned in the original description (Plötz 1882b). Therefore, this specimen might have been the model for the drawing. The label [26:15.] corresponds to the number for *P. tyana* in Mabille's catalog, where the locality for this species is given as "Sao-Paulo" [Brazil] (Mabille 1903), the same locality is listed on the unpublished Plötz's drawing, according to Godman (1907). Therefore, we infer that the type locality of *P. tyana* is in Brazil: São Paulo. The lectotype is missing its abdomen and both antennae. Images of this specimen (Fig. 91g) photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15032D11, GenBank PV550034, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCAGGAATAGTAGGAACATCTTTAAGTTTACTTATTCGATCCGAATTAGGAGCCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCCTTAACTTTATTAATTTCAAGAAGTATCGTAGAAAATGGTGCCGGAACAGGTTGAACTGTATACCCCCCTTTATCAGCTAATATTGC
CCATCAAGGTTCTTCCGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGTATCTCATCTATTTTAGGAGCTATTAATTTTATTACAACTATTATCAATATACGAATTAATAATTTATTA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCTTTACTTTTACTATTATCTTTACCAGTTCTAGCAGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACTT
CCTTTTTTGATCCTGCTGGAGGAGGAGACCCAATTTTATATCAACATTTATTT

Second, we found only one syntype for each of the remaining three taxa discussed here. For two of them, Godman's (1907) copies (in BMNH and USNM) of Plötz's unpublished drawing agree well with the original description and syntype specimens. However, the drawing of *Arteurotia demetrius* Plötz, 1882 (type locality in Brazil) (Fig. 91j) does not, and is so unusual that neither Godman (1907) nor Evans (1953) was able to associate a specimen with the drawing. The original description refers to specimens with the number 5912 in Berlin. Only one specimen (Fig. 91i) was listed for No. 5912 in the catalog of the MFNB historical collections. This specimen agrees with the original description translated here as: "No hyaline spots. Brown, forewing above with 2 darker, slightly curved crossbands, beneath at the costal margin passed the middle with 3 gray spots. Hindwing beneath predominantly gray, the costal margin [area] and 3 fading bands are brown" (Plötz 1882b). Conversely, the drawing shows 3 gray bands rather than spots (as in the specimen) on the ventral forewing, and brown with grayish cross-rays on the ventral hindwing, quite different from the specimen and the description. Nevertheless, out of syntypes of all these names we were able to find, the drawing of *A. demetrius* is most similar to the specimen No. 5912, because this specimen has the most extensive violaceous gray overscaling on ventral hindwing (Fig. 91i). Overall, we have no reason to doubt the status of the specimen No. 5912 as a syntype and hypothesize that Godman's copy of Plötz's drawing t[afel]. 205 is inaccurate (Fig. 91i vs. j). We doubt that the original drawing was any more accurate because the illustration of *A. demetrius* in Draudt (1921–1924), which is likely to be an independent copy of the original Plötz's drawing, is more similar to Godman's copy than to the syntype.

To stabilize nomenclature and define the name *A. demetrius* objectively, N.V.G. hereby designates a syntype in the MFNB collection that is shown in Fig. 91i and bears the following eight labels (1st red, 4th green, others white; 3rd, 4th and 5th handwritten, others printed with handwritten text shown in italics): [Type], [5912], [demetrius | Pl. | type], [Brasil. Bescke], [Gen. prep. | Mielke 1979], [Genital-Unters. | Nr. *4712* | Zool.Mus.Berlin], [{QR Code} http://coll.mfn-berlin.de/u/ | 940ba2], [DNA sample ID: | NVG-15032E12 | c/o Nick V. Grishin] as the **lectotype** of *Arteurotia demetrius* Plötz, 1882. The number 5912 on the 2nd label refers to a specimen lot documented in the catalog of historical collections. Under the entry 5912, the catalog lists a single specimen of an undetermined species collected in Brazil by Bescke. We guess that it was probably collected near Rio de Janeiro, because Bescke collected there. This general locality is also consistent with the results of genomic sequencing, placing the lectotype among specimens from that region. The lectotype has a nick in the middle of the outer margin of the right hindwing and some damage at the outer margin of the left forewing near the tornus. Images of this specimen (Fig. 91i) photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15032E12, GenBank PV550035, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCAGGAATAGTAGGAACATCTTTAAGTTTACTTATTCGATCCGAATTAGGAGCCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCCTTAACTTTATTAATTTCAAGAAGTATCGTAGAAAATGGTGCAGGAACAGGTTGAACTGTATACCCCCCTTTATCAGCTAATATTGC
CCATCAAGGTTCTTCCGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGTATCTCATCTATTTTAGGAGCTATTAATTTTATTACAACTATTATCAATATACGAATTAATAATTTATTA
TTTGATCAAATACCTTTATTTATTTGAGCAGTAGGAATTACAGCTTTACTTTTACTATTATCTTTACCAGTTCTAGCAGGAGCTATTACTATATTACTAACTGATCGTAATTTAAATACTT
CCTTTTTTGATCCTGCTGGAGGAGGAGACCCAATTTTATATCAACATTTATTT

Next, lectotypes of the remaining two taxa are designated. To stabilize nomenclature and define the name *Pellicia violacea* Mabille, 1891 (type locality in Brazil) objectively, N.V.G. hereby designates a syntype in the MFNB collection that bears the following ten labels (1st and 3rd shades of purple, others white; 3rd, 4th, 5th, and 7th handwritten, others printed with handwritten text shown in italics): [Origin.], [Coll. H.—Sch | *Brasilien*], [arteu.violacea | ♂ type Mab.], [ab Meno | Mab.? | (ich habe Origin.) | (Mab.)], [Rubescens | Plötz | violacea | Mab.], [Coll. | Staudinger], [Gen. prep. | Mielke 1979], [Genital-Unters. | Nr. *4711* | Zool.Mus.Berlin], [{QR Code} http://coll.mfn-berlin.de/u/ | 44a098], [DNA sample ID: | NVG-15034E05 | c/o Nick V. Grishin] as the **lectotype** of *Pellicia violacea* Mabille, 1891. The 3rd and the 4th labels are in Mabille's and Staudinger's handwriting, respectively. The lectotype is missing its right hindwing, which is placed in a small triangular envelope pinned with the labels. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). Genomic comparison suggests that the type locality of *P. violacea* is likely in Rio de Janeiro, Brazil. The COI barcode sequence of the lectotype, sample NVG-15034E05, GenBank PV550036, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCAGGAATAGTAGGAACATCTTTAAGTTTACTTATTCGATCCGAATTAGGAGCCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCCTTAACTTTATTAATTTCAAGAAGTATCGTAGAAAATGGTGCCGGAACAGGTTGAACTGTATACCCCCCTTTATCAGCTAATATTGC
CCATCAAGGTTCTTCCGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGTATCTCATCTATTTTAGGAGCTATTAATTTTATTACAACTATTATCAATATACGAATTAATAATTTATTA
TTTGATCAAATACCTTTATTTATTTGAGCAGTAGGAATTACAGCTTTACTTTTACTATTATCTTTACCAGTTCTAGCAGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACTT
CCTTTTTTGATCCTGCTGGAGGAGGAGACCCAATTTTATATCAACATTTATTT

To stabilize nomenclature and define the name *Pellicia vecina* Schaus, 1902 (type locality Brazil: Rio de Janeiro, Petropolis) objectively, N.V.G. hereby designates a syntype in the USNM collection that bears the following six labels (4th red, others white; 3rd handwritten, others printed with handwritten text shown in italics): [Petropolis, | Brazil.], [Collection | W.Schaus], [Pellicia | vecina | type Schs], [Type | No. *5977* | U. S. N. M.], [GENITALIA NO. | *1394* | J.M.Burns 1976], [USNMENT | {QR Code} 00913108] as the **lectotype** of *Pellicia vecina* Schaus, 1902. The lectotype is missing a section of the right hindwing at the tornus and a smaller segment on the left hindwing at the outer margin near the tornus. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-18061C10, GenBank PV550037, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCAGGAATAGTAGGAACATCTTTAAGTTTACTTATTCGATCCGAATTAGGAGCCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCCTTAACTTTATTAATTTCAAGAAGTATCGTAGAAAATGGTGCAGGAACAGGTTGAACTGTATACCCCCCTTTATCAGCTAATATTGC
CCATCAAGGTTCTTCCGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGTATCTCATCTATTTTAGGAGCTATTAATTTTATTACAACTATTATCAATATACGAATTAATAATTTATTA
TTTGATCAAATACCTTTATTTATTTGAGCAGTAGGAATTACAGCTTTACTTTTACTATTATCTTTACCAGTTCTAGCAGGAGCTATTACTATATTACTAACTGATCGTAATTTAAATACTT
CCTTTTTTGATCCTGCTGGAGGAGGAGACCCAATTTTATATCAACATTTATTT

Arteurotia demetrius Plötz, 1882 and *Pellicia vecina* Schaus, 1902 are junior subjective synonyms of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882

Genomic analysis reveals that in addition to *Pellicia violacea* Mabille, 1891 (type locality in Brazil, lectotype sequenced as NVG-15034E05), which is currently treated as a junior subjective synonym of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882 (type locality in South America, probably in Brazil: São Paulo, lectotype sequenced as NVG-15032D11), lectotypes of *Arteurotia demetrius* Plötz, 1882 (type locality in Brazil, probably Rio de Janeiro, NVG-15032E12) and *Pellicia vecina* Schaus, 1902 (type locality Brazil: Rio de Janeiro, Petropolis, NVG-18061C10) cluster closely with the lectotype of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882 (type locality in South America, NVG-15032D11) and another specimen from Paraguay identified as *P. vecina* (NVG-18061E08) (Fig. 90). All these lectotypes were likely collected in Southeast Brazil. Therefore, we propose that *Arteurotia demetrius* Plötz, 1882, **syn. nov.** and *Pellicia vecina* Schaus, 1902 **syn. nov.** are junior subjective synonyms of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882. This is the species that Evans (1953) called *P. vecina* because he misidentified *P. tyana* and could not identify *A. demetrius*, but described an (inaccurate) drawing of it copied from Plötz's original drawing t. 205 (Godman 1907) and reproduced here as Fig. 91j. It is unknown if the original drawing was more accurate.

Pellicia (*Hemipteris*) *fumida* Mabille, 1889 and *Pellicia* (*Hemipteris*) *aequatoria* Williams & Bell, 1939 are valid species distinct from *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882

We conclude that the specimen in the MFNB collection that bears the following seven labels (1st purple, others white; 2nd to 3rd handwritten, others printed with handwritten text shown in italics): [Origin.], [Itaituba | 86 Hhn.], [hemipteris | fumida Mab. | ♂], [Fumida | Mab.], [GEN.PREP., | MIELKE *1996*], [{QR Code} http://coll.mfn-berlin.de/u/ | 940ba3], [DNA sample ID: | NVG-15032F01 | c/o Nick V. Grishin] is the holotype of *Hemipteris fumida* Mabille, 1889. It agrees with the original description, and according to its label, the holotype was collected in Brazil: Pará, Itaituba by Hahnel in 1886. The 3rd label is in Mabille's handwriting. The holotype is an aberrant specimen with hindwings not fully expanded and a poorly developed pattern of spots and bands on the dorsal side of wings, with darker scaling along the veins standing out. Images of the holotype photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the holotype, sample NVG-15032F01, GenBank PV550038, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCAGGAATAGTAGGAACATCCTTAAGTTTACTTATTCGATCTGAATTAGGTACTCCTGGTTCTTTAATTGGAGATGATCAAATTTATAACACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATCATAATTGGTGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCTCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCTTTAACTTTATTAATTTCAAGAAGTATTGTAGAAAATGGTGCTGGAACTGGTTGAACTGTTTATCCTCCTTTATCAGCTAATATTGC
CCATCAAGGATCCTCTGTTGATTTAGCAATTTTTTCATTACATTTAGCAGGTATTTCCTCTATTTTAGGTGCTATTAATTTTATTACAACTATTATCAATATACGAGTTAATAATTTATTA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCTTTACTTTTATTATTATCATTACCAGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGTAATTTAAATACAT
CTTTTTTCGACCCTGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTC

Genomic analysis of the holotypes of *Hemipteris fumida* Mabille, 1889 (type locality in Brazil: Pará, Itaituba, sequenced as NVG-15032F01) (Fig. 90 orange) and *Pellicia aequatoria* Williams & Bell, 1939 (type locality in Ecuador, sequenced as NVG-18024D05) (Fig. 90 pink) currently treated as a junior subjective synonyms of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882 (type locality in South America, lectotype sequenced as NVG-15032D11) reveals that all three taxa belong to different clades and the former two are not closely associated with any other species. Therefore, we propose that *Pellicia* (*Hemipteris*) *fumida* Mabille, 1889, **stat. rest.** and *Pellicia* (*Hemipteris*) *aequatoria* Williams & Bell, 1939, **stat. rest.** are valid species distinct from *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882.

Pellicia (*Hemipteris*) *toza* Evans, 1953 is a species distinct from *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882

Genomic analysis reveals that a specimen from Panama identified by Bell through genitalia inspection (slide G1366) as *Pellicia tyana toza* Evans, 1953 (type locality in Colombia, Magdalena Valley),

sequenced as NVG-18019H06, and two other Panamanian specimens (not shown) are not monophyletic with *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882 (type locality in Brazil, likely São Paulo, lectotype sequenced as NVG-15032D11), which Evans (1953) misidentified, and instead are closely related to *Pellicia* (*Hemipteris*) *arina* Evans, 1953 (type locality in Mexico: Veracruz, Atoyac) being genetically differentiated from it at the species level (Fig. 90). Therefore, we propose that *Pellicia* (*Hemipteris*) *toza* Evans, 1953, **stat. nov.** is a species distinct from *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882.

Pellicia (*Hemipteris*) *naja* Steinhauser, 1989 is a species distinct from *Pellicia vecina* Schaus, 1902

Originally described and currently treated as a subspecies of *Pellicia vecina* Schaus, 1902 (type locality Brazil: Rio de Janeiro, Petropolis, lectotype sequenced as NVG-18061C10), which (see above) is a junior subjective synonym of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882 (type locality in Brazil, likely São Paulo, lectotype sequenced as NVG-15032D11), *Pellicia vecina naja* Steinhauser, 1989 (type locality in Peru: Madre de Dios, holotype sequenced as NVG-15038E08) is genetically differentiated from *P. tyana*—which is a species previously referred to as *P. vecina*—at the species level (Fig. 90); e.g., their COI barcodes differ by 2% (13 bp). Therefore, given that we could not associate any older name with it, we propose that *Pellicia* (*Hemipteris*) *naja* Steinhauser, 1989, **stat. nov.** is a species distinct from *Pellicia vecina* Schaus, 1902.

Pellicia (*Hemipteris*) *cina* Grishin, new species

http://zoobank.org/B301C9F0-F5CA-4B5D-9339-6064F08E7E66

(Figs. 90 part, 92–93)

Definition and diagnosis. Genomic analysis reveals that a specimen from Rondônia, Brazil, identified as *Pellicia vecina cyanea* Biezanko & O. Mielke, 1973 (type locality Brazil: Rio Grande do Sul, Pelotas), currently treated as a junior subjective synonym of *Pellicia vecina* Schaus, 1902 (type locality Brazil: Rio de Janeiro, Petropolis, lectotype sequenced as NVG-18061C10), which furthermore (see above) becomes a junior subjective synonym of *Pellicia* (*Hemipteris*) *tyana* Plötz, 1882 (type locality in Brazil, likely São Paulo, lectotype sequenced as NVG-15032D11) due to previous misidentification of *P. tyana*, is genetically differentiated from and not even monophyletic with *P. vecina* and *Pellicia tyana*, and is sister to *Pellicia* (*Hemipteris*) *naja* Steinhauser, 1989, **stat. nov.** (type locality in Peru: Madre de Dios, holotype sequenced as NVG-15038E08) differing from it at the species level (Fig. 90), and, therefore, this specimen represents a new species. This new species keys to "*Pellicia vecina najaoides*" (E.21.5.(a)) in Evans (1953), which is misspelled, misidentified, and was redescribed by Steinhauser as *P. vecina naja*, but differs from its relatives by the following combination of characters: dorsal forewing has violet gloss between brown bands, dorsal hindwing is dark-brown with 2 prominent paler bars in the discal cell and paler costal margin, ventral hindwing is brown with paler apex (but not as pale as in *P. naja*) and paler area along the inner margin, ventral hindwing is brown with paler brown posterior half, paler towards tornus, but not whitish, and with broader than in *P. naja* dark-brown bands and a prominent dark spot at the tornus; left harpe is armed with prominent teeth on the anterior margin and a sharper, longer tooth directed inwards from the ampulla (Fig. 93). Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly527.12.3:C156T, aly420.21.9:C36T, aly204.15.1:T279C, aly1113.7.3:T54C, aly1113.7.3:G78T, however, the COI barcode does not distinguish this species from *P. naja*.

Barcode sequence of the holotype. Sample NVG-23053D08, GenBank PV550039, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGATCAGGAATAGTAGGAACATCTTTAAGTTTACTTATTCGATCCGAATTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCCTTAACTTTATTAATTTCAAGAAGTATCGTAGAAAATGGTGCCGGAACAGGTTGAACTGTATACCCCCCTTTGTCAGCTAATATTGC
TCATCAAGGTTCTTCCGTTGATTTAGCAATTTTTTCCTTACACTTAGCAGGTATCTCATCTATTTTAGGAGCTATTAACTTTATTACAACTATTATCAATATACGAGTTAATAATTTATTA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGAATTACAGCTTTACTTTTACTATTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTATTAACTGATCGTAATTTAAATACTT
CCTTTTTTGATCCTGCTGGAGGAGGGGATCCAATTTTATATCAACATTTATTT

Fig. 92. *Pellicia* (*Hemipteris*) *cina* **sp. n.** holotype ♂ NVG-23053D08 in dorsal (left) and ventral (right) views, data in text.

Fig. 93. Male genitalia of *Pellicia* (*Hemipteris*) *cina* **sp. n.** holotype NVG-23053D08 (data in text) in different views: **a)** right lateral, **b)** left lateral, **c)** right posterolateral, **d)** left posterolateral, **e)** dorsal, and **f)** posterior tilted dorsad.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 92 (genitalia Fig. 93), bears the following six printed (text in italics handwritten) rectangular labels (4th brownish yellow and the last red): [BRASIL: Rondônia | 62 km S Ariquemes | linea C-20, 7 km E | B-65, Fazenda | Rancho Grande | 14 November 1990 | leg. D&J Lindsley], [Genetalic Vial | GTA-*875*], [Pellicia vecina | cyanea Biezanko & | Mielke | det. GT Austin 199*1*], [photographed | G.T. Austin & J. P. Brock | March 1992], [DNA sample ID: | NVG-23053D08 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Pellicia (Hemipteris) | cina

Grishin]. **Paratype:** 1♂ NVG-24083A08 the same data as the holotype but 7-Nov-1991, G. T. Austin leg., genitalia vial GTA-2138.

Type locality. Brazil: Rondônia, 62 km south of Ariquemes, linha C-20, 7 km east of B-65, Fazenda Rancho Grande.

Etymology. The name is formed from the name of a related taxon, *vecina*, made shorter for its more northern relative. The name is treated as a feminine noun in apposition.

Distribution. Currently known only from Rondônia, Brazil.

Lingering questions about *Pellicia* Herrich-Schäffer, 1870

Genomic analysis of many primary type specimens in the genus *Pellicia* Herrich-Schäffer, 1870 (type species *Pellicia dimidiata* Herrich-Schäffer, 1870) reveals their taxonomic identity and previous misidentifications. As a result, we propose many new synonymies and reinstate several species. However, working with a small sample of specimens and not being able to find primary types of some taxa leaves us with several unanswered questions to address.

First, as we hypothesized (Zhang et al. 2023c), North and Central American specimens previously identified as *P. dimidiata* Herrich-Schäffer, 1870 are distinct from South American specimens at the species level. We attributed the name *P. dimidiata* to the South American species based on the taxonomic identity of the syntype from Venezuela, but refrained from designating this syntype a lectotype, searching for possible syntypes from "Mexico". We used the name *Pellicia bilinea* Mabille, 1889 (type locality in Panama: Chiriquí) as valid for the North and Central American species as the oldest name with a strongly supported taxonomic identity based on a syntype of *P. bilinea* we located. Here, taking the next step to stabilize nomenclature and define this name objectively, N.V.G. hereby designates a syntype in the MFNB collection that bears the following nine labels (1st purple, others white; 3rd to 6th handwritten, others printed with handwritten text shown in italics): [Origin.], [Chiriqui | Ribbe], [Pellicia | bilinea | Mab.], [Pellicia | Bilinea | Mab.], [Bilinea | Mab.], [Gen. prep. | Mielke 1979], [Genital-Unters. | Nr. *4713* | Zool.Mus.Berlin], [{QR Code} http://coll.mfn-berlin.de/u/ | 940b91], [DNA sample ID: | NVG-15032E01 | c/o Nick V. Grishin] as the **lectotype** of *Pellicia bilinea* Mabille, 1889. According to its label, the lectotype was collected in Chiriquí, Panama, by Carl Ribbe. The 3rd and the 4th labels are in Mabille's and Staudinger's handwriting, respectively. The lectotype has minor damage to its left hindwing fringe in the middle and at the tornus. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15032E01, GenBank PV550040, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATTTGATCTGGAATAGTAGGAACATCATTAAGTTTAATTATTCGATCCGAATTAGGTACCCCTAGATCTTTTATTGGAGATGATCAAATTTATAATACC
ATTGTAACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCTCCTGATATAGCTTTTCCCCGAA
TAAATAACATAAGATTTTGACTTTTACCTCCTTCTATTACTCTATTAATTTCAAGAAGTTTTGTAGAAAATGGTGTTGGTACAGGTTGAACTGTTTATCCTCCTTTATCTGCTAATATTGC
TCATCAAGGTTCTTCTGTAGATTTAGCAATTTTTTCTTTACATTTAGCTGGTATTTCATCTATTTTAGGTGCTATTAATTTTATTACAACCATTATTAATATACGAATTAACAATTTATTA
TTTGATCAAATACCTTTATTTATTTGAGCTGTTGGAATTACAGCTTTACTTTTATTACTATCTCTACCAGTTTTAGCTGGAGCTATTACCATATTATTAACTGATCGAAATCTTAATACAT
CTTTTTTTGACCCTGCGGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

However, an older name, *Achlyodes nivonicus* Plötz, 1884 (type locality in Mexico) might apply to *P. bilinea* and become valid for this taxon. According to Godman (1907), *A. nivonicus* "is doubtless the female of" *P. dimidiata* (the name Godman used for Mexican specimens) and it was "figured from a damaged specimen" by Plötz, meaning that the illustrated syntype was a female from Mexico, appeared damaged, and was similar to *P. bilinea*. However, we are not positive about Godman's synonymy. The original description of *A. nivonicus* might equally well, if not better, apply to a female of *Viuria licisca* (Plötz, 1882) (type locality in Nicaragua, the name proposed for male specimen(s)), or even to some damaged female of a Mexican *Quadrus* (*Ouleus* Lindsey, 1925) resembling its type species *Quadrus* (*Ouleus*) *fridericus fridericus* (Geyer, 1832) (type locality in Suriname).

The description of *A. nivonicus* is brief and states (assembled from the key and translated): "Forewing without subapical hyaline spots. The outer margin of all wings is smooth and rounded. Hindwing beneath evenly brownish gray [meaning not paler towards tornus] with dark bands. Upperside black-brown, forewing with three even darker bands. The outer band of the forewing is broken up into

spots" (Plötz 1884). The closest species it was compared to was *Achlyodes thiena* Plötz, 1884 (no locality data), differing by the last sentence: "The outer band of the forewing is complete, very indistinct." In MFNB, we located a likely syntype of *A. thiena*, which is *Q. fridericus fridericus*, as currently treated, a dark species as described by Plötz, with a weakly defined continuous dark band near the dorsal forewing margin. Therefore, *A. nivonicus* should have been dark as well, but *P. bilinea* females typically have paler brown ground color and narrower dark bands, thus not resembling *Q. fridericus*.

Conversely, *V. licisca* females, which are patterned similarly to *P. bilinea*, are darker, with broader dark bands and sometimes with nearly dark-brown hindwings above (no pattern was mentioned by Plötz for the hindwing, and the hindwing of *A. thiena* syntype is nearly uniformly dark brown). Both *P. bilinea* and *V. licisca* may have a dark marginal band broken up into spots. It is also possible that it might have been a species known today as *Quadrus* (*Ouleus*) *salvina* (Evans, 1953), which is somewhat similar to *Q. fridericus*, or some mislabeled and damaged female of another species. To solve this problem, we are searching for syntypes of *A. nivonicus* and specimens from Mexico that agree with all the information about this taxon as candidates for a neotype. Presently, we tentatively place *Achlyodes nivonicus* Plötz, 1884 as a junior subjective synonym of *Viuria licisca* (Plötz, 1882), because the latter species agrees best with the original description of the former.

Second, we sequenced rather few specimens of *Pellicia*. While our results confidently resolve the taxonomic identity of primary type specimens and are sufficient to support our major conclusion, further studies are expected to clarify species vs. subspecies boundaries in *Pellicia*. We observe noticeable genitalic differences for taxa that are rather similar genetically. Sequencing a larger series of specimens of each taxon will enable us to study intra- vs. interspecies genetic differentiation and explain the apparent lack of COI barcode differences and relatively small nuclear genome differences between several species distinct in genitalia.

Third, adding not yet sequenced taxa of *Pellicia* to the analysis will help us find their place in the taxonomic list and may result in further synonymization of names proposed by Evans (1953), who misidentified the majority of *Pellicia* taxa, or reinstatement of some species currently treated as synonyms.

Gorgopas trochicuz Grishin, new species

http://zoobank.org/DB2C8820-6477-4AF8-B492-4A0E33E7F758

(Figs. 94 part, 95, 96a–c)

Definition and diagnosis. Genomic analysis reveals that two specimens from Cuzco, Peru, identified as *Gorgopas trochilus* (Hopffer, 1874) (type locality in Bolivia, holotype sequenced as NVG-15032D07) are genetically differentiated from it at the species level in the nuclear genome (Fig. 94), e.g., an F_{st} value of 0.3, while not differing significantly in the COI barcode (0.3%, 2 bp only), and, therefore, represent a new

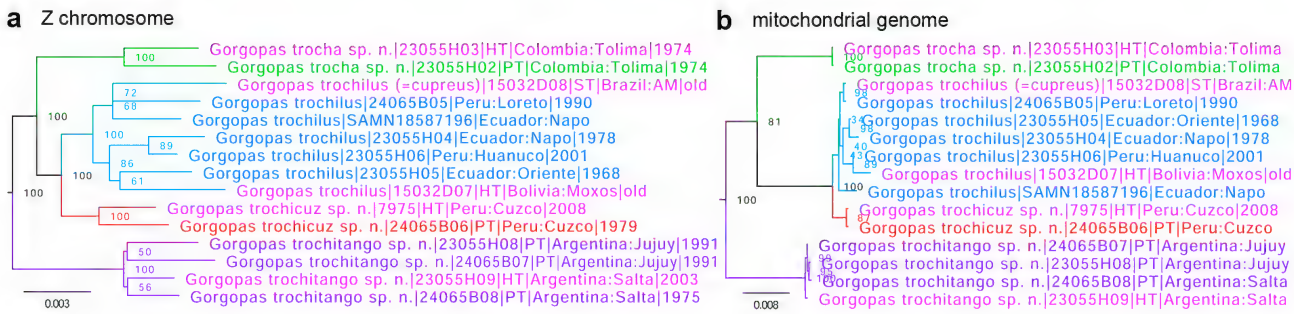


Fig. 94. Phylogenetic trees of selected *Gorgopas* species constructed from protein-coding regions in: **a)** the Z chromosome, based on 336,096 positions, and **b)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species are shown in different colors: *G. trocha* **sp. n.** (green), *G. trochilus* (blue), *G. trochicuz* **sp. n.** (red), and *G. trochitango* **sp. n.** (purple). Primary type specimens are labeled in magenta. The sequence of SAMN18587196 is taken from the alignment provided in Kawahara et al. (2023).

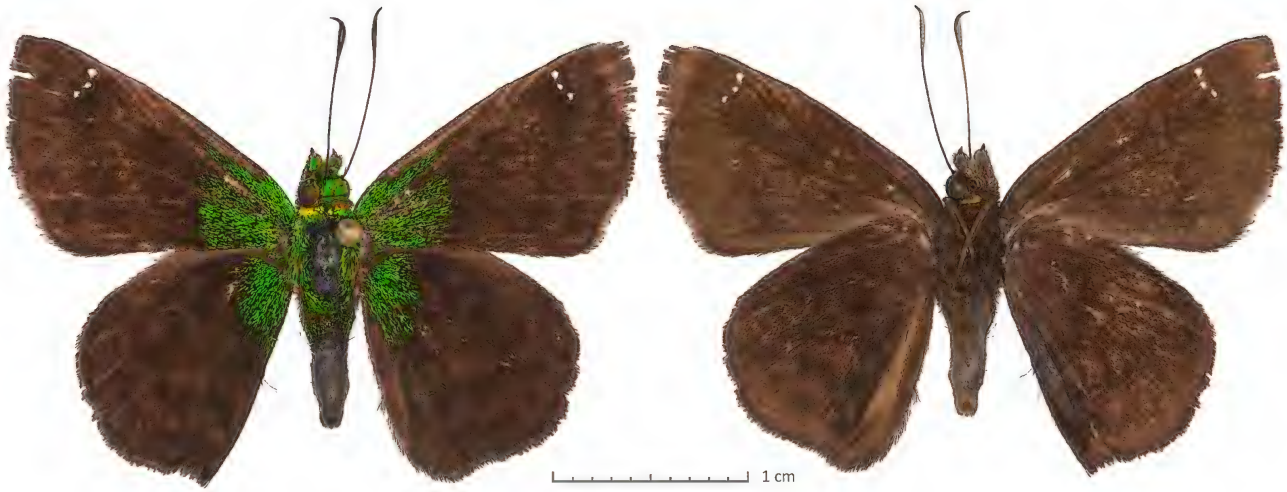


Fig. 95. *Gorgopas trochicuz* **sp. n.** holotype ♂ NVG-7975 in dorsal (left) and ventral (right) views, data in text. All *Gorgopas* specimens (Figs. 95, 97, 99) are shown at the same scale to facilitate comparisons.

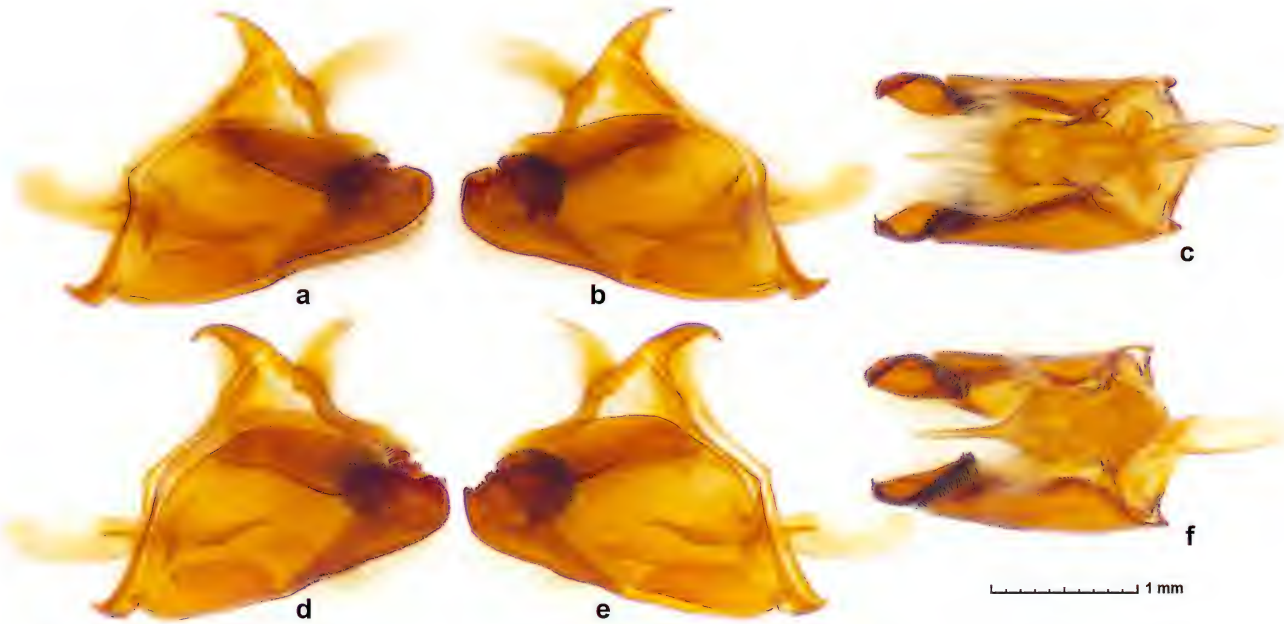


Fig. 96. Genitalia of *Gorgopas*: **a–c)** *G. trochicuz* **sp. n.** holotype ♂ NVG-7975 data in text and **d–f)** *G. trochilus* ♂ NVG-23055H04 Ecuador, Napo, Misahuallí environs, 300 m, Oct-Nov-1978, N. Venedictoff leg., vial NVG250517-05 [MGCL] in different views: **a, d)** left lateral, **b, e)** right lateral, and **c, f)** dorsal.

species. This new species keys to *G. trochilus* (E.28.1) in Evans (1953) but differs from it by being darker, with a more diffuse pattern of paler spots on both sides of wings and by narrower valvae with a narrower folded-over region at the costa, smaller and less robust sclerotized inner lobes of harpe, in particular on the right valva (Fig. 96a–c)—this lobe is larger and more closely connected with the right harpe in *G. trochilus* (Fig. 96d–f), which has a broader and rounder right valva, mainly due to a more strongly developed costa with a broader folded-over region. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly383.14.3:G855C, aly383.14.3:G888A, aly1042.34.1:G71A, aly1042.34.1:A167G, aly216.74.1:C48T, and may not confidently differ from *G.*

trochilus in the COI barcode, although the following combination of base pairs identifies sequenced specimens: A34A, A70A, T400T, T595T, 616T.

Barcode sequence of the holotype. Sample NVG-7975, GenBank PV550041, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGATCTGGAATAATTGGAACTTCTTTAAGTATTCTTATTCGATCAGAATTAGGTACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTCTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCAGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTCTTATATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACTGTTTACCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGTTCTTCAGTAGATTTAACTATTTTTTCTCTTCATTTAGCAGGTATTTCTTCTATTTTAGGAGCAATTAATTTTATTACAACTATTATTAATATACGAATTAATAAATTATCA
TTTGATCAAATATCTTTATTTATTTGAGGTGTAGGAATTACTGCATTACTTCTATTATTATCTTTACCAGTTTTAGCAGGTGCTATTACTATATTATTAACTGATCGAAATCTTAACACAT
CTTTTTTTGATCCTTCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 95 (genitalia Fig. 96a–c), bears the following five printed (text in italics handwritten) rectangular labels, four white: [PERU:Cuzco,564m. | Pilcopata | Cosnipata Rd 021 | 15-XI-2008 Kinyon], [DNA sample ID: | NVG-7975 | c/o Nick V. Grishin], [genitalia | NVG170207-60 | Nick V. Grishin], [USNMENT | {QR Code} | 01321815], and one red [HOLOTYPE ♂ | Gorgopas | trochicuz Grishin]. **Paratype:** 1♂ NVG-24065B06 Peru, Cuzco, Pilcopata, 600 m, 15-18-Dec-1979, J. B. Heppner leg. [MGCL].

Type locality. Peru: Cuzco, Cosñipata Road, Pilcopata, elevation 564 m.

Etymology. The name is a fusion: *trochi*[lus] + *Cuz*[co} (for the type locality) and is treated as a noun in apposition.

Distribution. Currently known only from the type locality, which is to the northeast of the Andes in southern Peru.

Gorgopas trocha Grishin, new species

http://zoobank.org/69AF3910-A35A-474E-A0A1-1881F9DBB43F

(Figs. 94 part, 97–98)

Definition and diagnosis. In addition to the new species described above, specimens from Colombia are genetically differentiated from *Gorgopas trochilus* (Hopffer, 1874) (type locality in Bolivia, holotype sequenced as NVG-15032D07) at the species level (Fig. 94); e.g., their F_{st}/COI barcode differences are 0.45/1.5% (10 bp), and, therefore, represent a new species. This new species keys to *G. trochilus* (E.28.1) in Evans (1953) but differs from it and the new species described above by being paler, with a more strongly defined contrast between darker brown and paler brown areas giving the dorsal hindwing a checkered appearance, somewhat weaker green overscaling, broader wings, more trapezoidal hindwings, broader valvae and even stronger defined sclerotized inner lobe of harpe. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1139.17.3:A54G, aly1139.17.3:G60A, aly1042.31.2:C89T, aly1042.31.2:A102T, aly96.3.7:T51C; and COI barcode: T46C, 220C, C340C, T400C, T415A, C536T.

Barcode sequence of the holotype. Sample NVG-23055H03, GenBank PV550042, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGATCTGGAATAATTGGAACCTCTTTAAGTATTCTTATTCGATCAGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTCTTTATAGTAATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCAGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTCTTATATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACTGTTTACCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGTTCTTCAGTAGATTTAACTATTTTTTCCCTTCATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATTAATTTTATTACAACTATTATTAATATACGAATTAATAAATTATCA
TTTGATCAAATATCCTTATTTATTTGAGCTGTAGGAATTACTGCATTACTTTTATTATTATCTTTACCAGTTTTAGCAGGTGCAATTACTATATTATTAACTGATCGAAATCTTAATACAT
CTTTTTTTGATCCTTCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 97 (genitalia in Fig. 98), bears the following six printed rectangular labels, five white: [COLOMBIA: TOLIMA | La Marina area, Rio | Ambeima, 1600-1700 m. | 7.vi.1974 | S. & L. Steinhauser], [A. C. Allyn | Acc. 1974-23], [DNA sample ID: | NVG-23055H03 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24065B04 | c/o Nick V. Grishin], [genitalia: | NVG241111-16 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Gorgopas | trocha Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratype:** 1♂ NVG-23055H02 the same data as the holotype but collected on 12-Jun-1974.

Type locality. Colombia: Tolima, La Marina area, Rio Ambeima, elevation 1600–1700 m.

Fig. 97. *Gorgopas trocha* **sp. n.** holotype ♂ NVG-23055H03 in dorsal (left) and ventral (right) views, data in text.

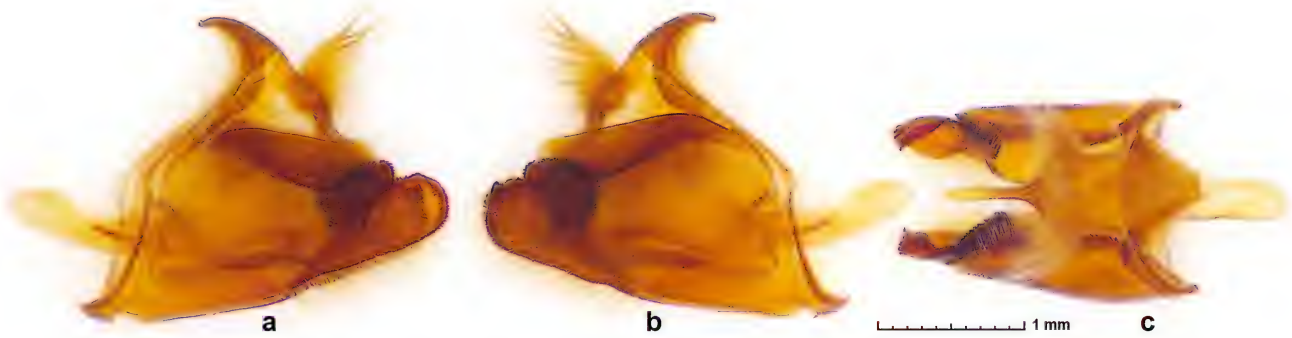


Fig. 98. Genitalia of *Gorgopas trocha* **sp. n.** holotype ♂ NVG-23055H03 in different views:
a) left lateral, **b)** right lateral, **c)** dorsal.

Etymology. The name is formed from the name of its relative, *G. trochilus*, made shorter to indicate the more northern distribution locality of this species, and is treated as a noun in apposition.

Distribution. Currently known only from Tolima in Colombia.

Gorgopas trochitango Grishin, new species

http://zoobank.org/DAAE3729-7B65-423B-BD81-052BBB2C6533

(Figs. 94 part, 99–100)

Definition and diagnosis. In addition to the two new species described above, specimens from Argentina are genetically differentiated from *Gorgopas trochilus* (Hopffer, 1874) (type locality in Bolivia, holotype sequenced as NVG-15032D07) at the species level (Fig. 94); e.g., their F_{st}/COI barcode differences are 0.51/1.7% (11 bp), and, therefore, represent a new species. This new species keys to *G. trochilus* (E.28.1) in Evans (1953) but differs from it and the two new species described above by being paler, with a more strongly defined contrast between darker brown and paler brown areas giving the dorsal hindwing a checkered appearance, significantly weaker green overscaling that on the hindwing is nearly vestigial and constrained to the very base, more pointed forewings, broader valvae with a slightly smaller and less distinct sclerotized inner lobe of harpe. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly251.9.2:G45A, aly251.9.2:G57A, aly320.2.32:C36T, aly320.2.32: G48A, aly1139.31.4:G1091T; and COI barcode: C187C, C340T, T382T, T499C, 598A.

Fig. 99. *Gorgopas trochitango* **sp. n.** holotype ♂ NVG-23055H09 in dorsal (left) and ventral (right) views, data in text.

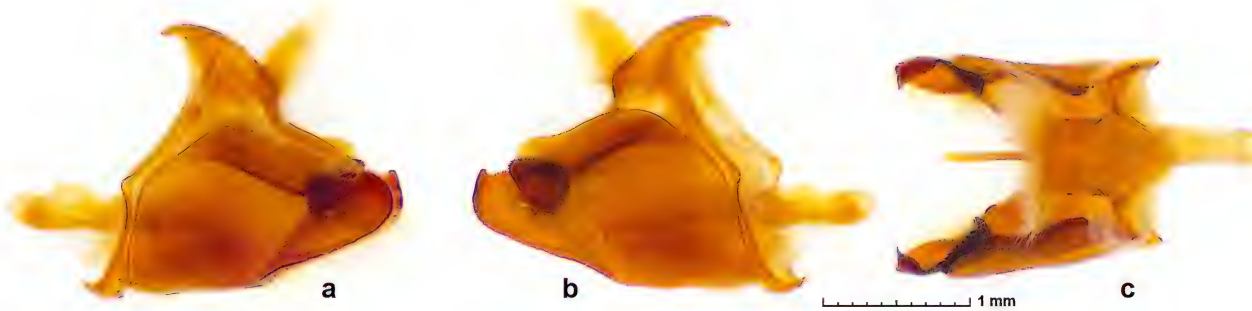


Fig. 100. Genitalia of *Gorgopas trochitango* **sp. n.** holotype ♂ NVG-23055H09 in different views: **a)** left lateral, **b)** right lateral, **c)** dorsal.

Barcode sequence of the holotype. Sample NVG-23055H09, GenBank PV550043, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGATCTGGAATAATTGGAACTTCTTTAAGTATTCTTATTCGATCAGAATTAGGAACTCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTCTTTATAGTAATACCAATTATAATTGGAGGATTCGGAAATTGATTAGTACCTTTAATATTAGGAGCCCCAGATATAGCTTTTCCTCGTA
TAAATAATATAAGATTTTGATTATTACCTCCTTCTCTTATATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACTGTTTATCCCCCTCTTTCAGCTAATATTGC
TCATCAAGGTTCTTCAGTTGATTTAACTATTTTTTCTCTTCATTTAGCAGGTATTTCTTCTATTTTAGGAGCAATTAATTTTATTACAACTATTATTAATATACGAATTAATAAATTATCA
TTTGATCAAATATCCTTATTTATTTGAGCTGTAGGAATTACTGCATTACTTCTATTATTATCTTTACCAGTTTTAGCAGGTGCAATTACTATATTATTAACTGATCGAAATCTAAATACAT
CTTTTTTTGACCCTTCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 99 (genitalia in Fig. 100), bears the following five printed rectangular labels, four white: [Baritú Lodge | Salta, Argentina | S22°37.953'; W64°26.612' | elevation 2112 ft. | November 17, 2003 | D.L Lindsley], [Gorgopas Godman&Salvin | tröchilus (Hopffer)], [D.L. Lindsley colln. | MGCL Accession | # 2008-20], [DNA sample ID: | NVG-23055H09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Gorgopas | trochitango Grishin]. An unnumbered vial with genitalia, likely dissected by D. L. Lindsley, is pinned between the labels of the holotype. **Paratypes:** 3♂♂ from Argentina, R. Eisele leg. [MGCL]: 2♂♂ NVG-24065B07 and NVG-23055H08 Jujuy, Ledesma, Calilegua, Rt. 83. 5–7.5 km W of Rt. 34, 550-600 m, 4-Apr-1991 and 1♂ NVG-24065B08 Salta, Sierra de Tartagal, Rio Yacuy, 14 km W of Rt. 34, 800 m, 10-Apr-1975.

Type locality. Argentina: Salta, Baritú Lodge, elevation 2112 ft, GPS −22.6326, −64.4435.

Etymology. The name is a fusion: *trochi*[lus] + *tango* (strongly associated with Argentina, for the type locality) and is treated as a noun in apposition.

Distribution. Currently known only from northern Argentina.

Lectotype designations for *Pholisora clytius* Godman & Salvin, 1897 and *Bolla semitincta* Dyar, 1924

Recently, we proposed that the genus *Clytius* Grishin, 2019 (type species *Pholisora clytius* Godman & Salvin, 1897) consists of five species: *Clytius clytius* (Godman & Salvin, 1897) (type locality in Mexico:

Nayarit, Tres Marias Island, syntype sequenced as NVG-18082E10), *Clytius semitincta* (Dyar, 1924) (type locality in Colima, syntypes sequenced as ♂ NVG-15109B06 and ♀ NVG-15109C12), *Clytius mattus* Grishin, 2024 (type locality USA: Hidalgo Co., Bentsen-Rio Grande Valley State Park, holotype sequenced as NVG-5486), *Clytius unifascia* (Mabille, 1889) (type locality Honduras, lectotype sequenced as NVG-15033G05), and *Clytius shola* (Evans, 1953) (type locality not specified, likely in Venezuela) (Zhang et al. 2022b; Zhang et al. 2024b).

To stabilize nomenclature and define the name *C. clytius* objectively, N.V.G. hereby designates a syntype in the BMNH collection, a male that bears the following twelve labels (first two and the last round, others rectangular; first two with a red circle on one side, last yellow, others white; 7th, 9th, and 12th handwritten, others printed): (Type), (Type) and on the other side of this label handwritten (H | 737), [Tres Marias Is., | W. Mexico. | Forrer.], [♂], [Sp. figured.], [B.C.A.Lep.Rhop. | Pholisora | clytius, | G.&S.], [Pholisora | clytius sp.n | Type Fig[d]], [Godman-Salvin | Coll. 1912.—23.], [D10] with genitalia pieces glued to this label, [{QR Code} | BMNH(E) 1669520], [MOLECULAR | 0247274691], (426) as the **lectotype** of *Pholisora clytius* Godman & Salvin, 1897. The lectotype's right hindwing has a tear at the outer margin near the apex where a tiny wing segment is folded down. Images of this specimen photographed by N.V.G. are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-18082E10, molecular NHMUK_0247274691, GenBank ON480064, PV550044, 658 base pairs, is:

AACTTTATACTTTATTTTTGGTATTTGATCTGGTATAGTAGGAACTTCTTTAAGTATATTAATTCGTTCTGAACTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCTTTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCCCCTTTATCAGCTAATATTGC
TCACCAAGGTTCTTCTGTAGATTTAGCCATTTTTTCATTACATTTAGCTGGAATTTCTTCTATTTTAGGTGCTATTAATTTTATTACAACTATTATTAATATACGAATTAATAATTTATCT
TTCGATCAAATACCTTTATTCGTATGAGCTGTAGGAATCACAGCTTTACTTTTACTTTTATCTCTACCAGTTTTAGCTGGAGCTATTACAATACTTTTAACTGATCGAAATCTTAATACAT
CTTTTTTTGATCCTGCTGGTGGAGGTGATCCTATTTTATATCAACATTTATTT

To stabilize nomenclature and define the name *C. semitincta* objectively, N.V.G. hereby designates a syntype in the USNM collection, a male that bears the following six rectangular labels (1st and 5th handwritten, others printed with handwritten text shown in italics; 4th red and others white): [Colima | Mex.], [Dec | *1922*], [RMuller| Collector], [TypeNo. | | U.S.N.M.] no type number is given on the label, [Bolla | semitincta | Type Dyar], [GENITALIA NO. | X- *32 14* | J.M.Burns 199*1*] as the **lectotype** of *Bolla semitincta* Dyar, 1924. The lectotype is missing the left antenna, has its head turned to the left, and both costal folds are partly opened from the base. Images of this specimen photographed by Bernard Hermier (and N.V.G.) are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15109B06, GenBank PV550045, 658 base pairs, is:

AACTTTATACTTTATTTTTGGTATTTGGTCTGGTATAGTAGGAACTTCTTTAAGAATATTAATTCGTTCTGAACTAGGAACCCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCCATTATAATTGGAGGATTCGGAAATTGATTAGTACCCCTTATATTAGGAGCCCCTGATATAGCTTTTCCCCGAA
TAAATAATATAAGATTTTGACTTTTACCTCCTTCTTTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCCCCTTTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTAGATTTAGCCATTTTTTCTTTACATTTAGCTGGAATTTCCTCTATTTTAGGTGCTATTAATTTTATTACAACTATTATTAATATGCGAATTAATAATTTATCT
TTCGATCAAATACCTTTATTTGTATGAGCTGTGGGAATTACAGCTTTACTTTTACTCTTATCTCTACCAGTTTTAGCTGGAGCTATTACAATACTTTTAACTGATCGAAATCTTAACACAT
CTTTTTTTGACCCTGCTGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Perus (*Perus*) *perus* Grishin, new species

http://zoobank.org/445F016E-851C-4B10-B4EC-2853F968CA89

(Figs. 101 part, 102, 103a–d)

Definition and diagnosis. Genomic analysis of specimens identified as *Perus* (*Perus*) *cordillerae* (Lindsey, 1925) (type locality Peru: Lima, Matucana, holotype sequenced as NVG-22043E08) reveals that they partition into two clades genetically differentiated at the species level (Fig. 101); e.g., their F_{st}/G_{min}/COI barcode differences are 0.36/0.01/1.4% (9 bp). One clade (Fig. 101 blue) contains the holotype of *P. cordillerae*, along with specimens from Ecuador, and corresponds to this species. The other clade with specimens from Peru represents a new species. This new species keys to "*Staphylus cordillerae*" (E.32.25) in Evans (1953) and was included by him in that taxon, but differs from it by a rounder, and more robust spiculate process (lobe-shaped) arising from the wider folded-over region of the valva near the ampulla (Fig. 103a, c)—this process is more elliptical in *P. cordillerae* and the folded-over region is narrower (Fig. 103e, j, k); a concave junction between the tegumen and the uncus in lateral view (Fig. 103a, c)—straighter in *P. cordillerae* (Fig. 103e, h); the central dark band on the dorsal forewing

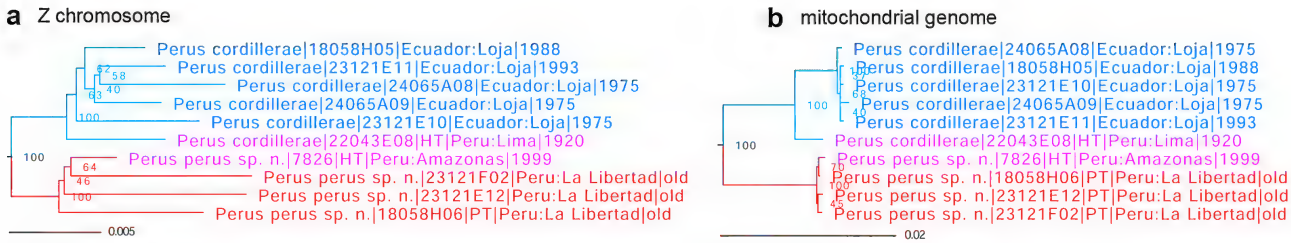


Fig. 101. Phylogenetic trees of *Perus* (*Perus*) *cordillerae* (blue) and *Perus* (*Perus*) *perus* **sp. n.** (red) constructed from protein-coding regions in: **a)** the Z chromosome, based on 315,390 positions, and **b)** the mitochondrial genome. Primary type specimens are labeled in magenta. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

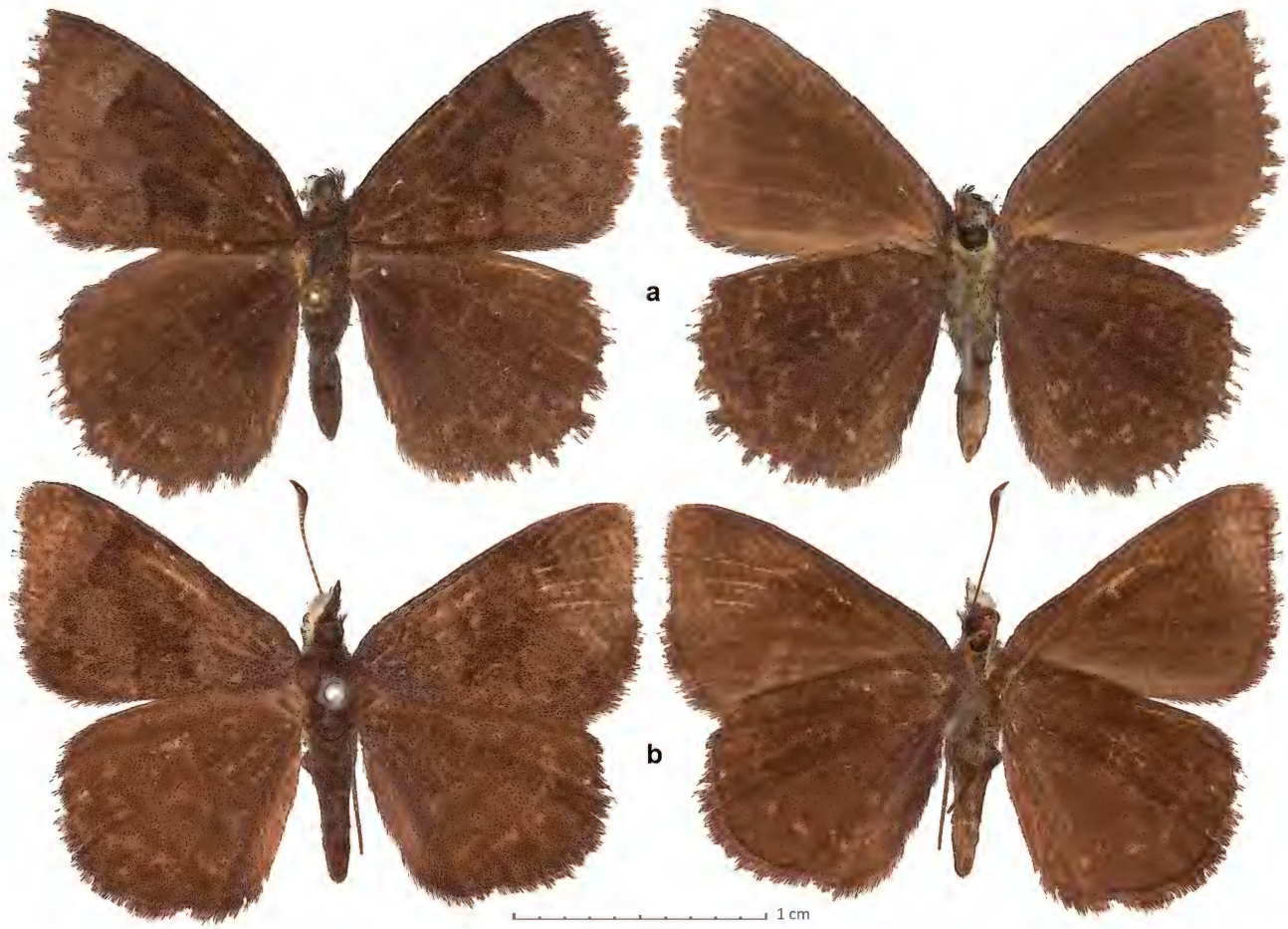


Fig. 102. *Perus* (*Perus*) *perus* **sp. n.** males in dorsal (left) and ventral (right) views, data in text: **a)** holotype NVG-7826 and **b)** paratype NVG-18058H06.

that is mostly uniformly colored, without a strongly developed pale bar in the discal cell within the band; more uniform and weaker at margins yellowish overscaling beneath; and a more weakly developed central pale spot on the ventral hindwing. Due to unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly671.23.3:C198T, aly1468.14.2:A42G, aly276561.5.1:T763A, aly276561.5.1:A1998T, aly6841.32.4:A777G; and COI barcode: A181G, A325T, 400T, T508A, T557C.

Barcode sequence of the holotype. Sample NVG-7826, GenBank PV550046, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGATCAGGTATAGTAGGAACTTCTTTAAGTATACTTATTCGATCTGAATTAGGAACACCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGGGGATTTGGAAACTGATTAGTACCTCTTATATTAGGAGCTCCTGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCTCCATCCCTTACATTATTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAACTGGATGAACTGTATATCCCCCTTTATCAGCTAATATTGC
CCATCAAGGTTCTTCTGTTGATTTAGCTATCTTCTCTCTTCATTTAGCAGGTATTTCTTCTATTTTAGGGGCAATTAATTTTATTACTACTATTATTAATATACGAATTAACAATTTATCA
TTTGATCAAATATCTTTATTTGTATGAGCAGTAGGAATTACAGCATTACTTTTATTATTATCCTTACCAGTTCTAGCTGGAGCTATTACTATACTTCTTACAGATCGTAATTTAAATACTT
CTTTTTTTGACCCTGCAGGAGGAGGAGATCCTATCTTATATCAACATTTATTT

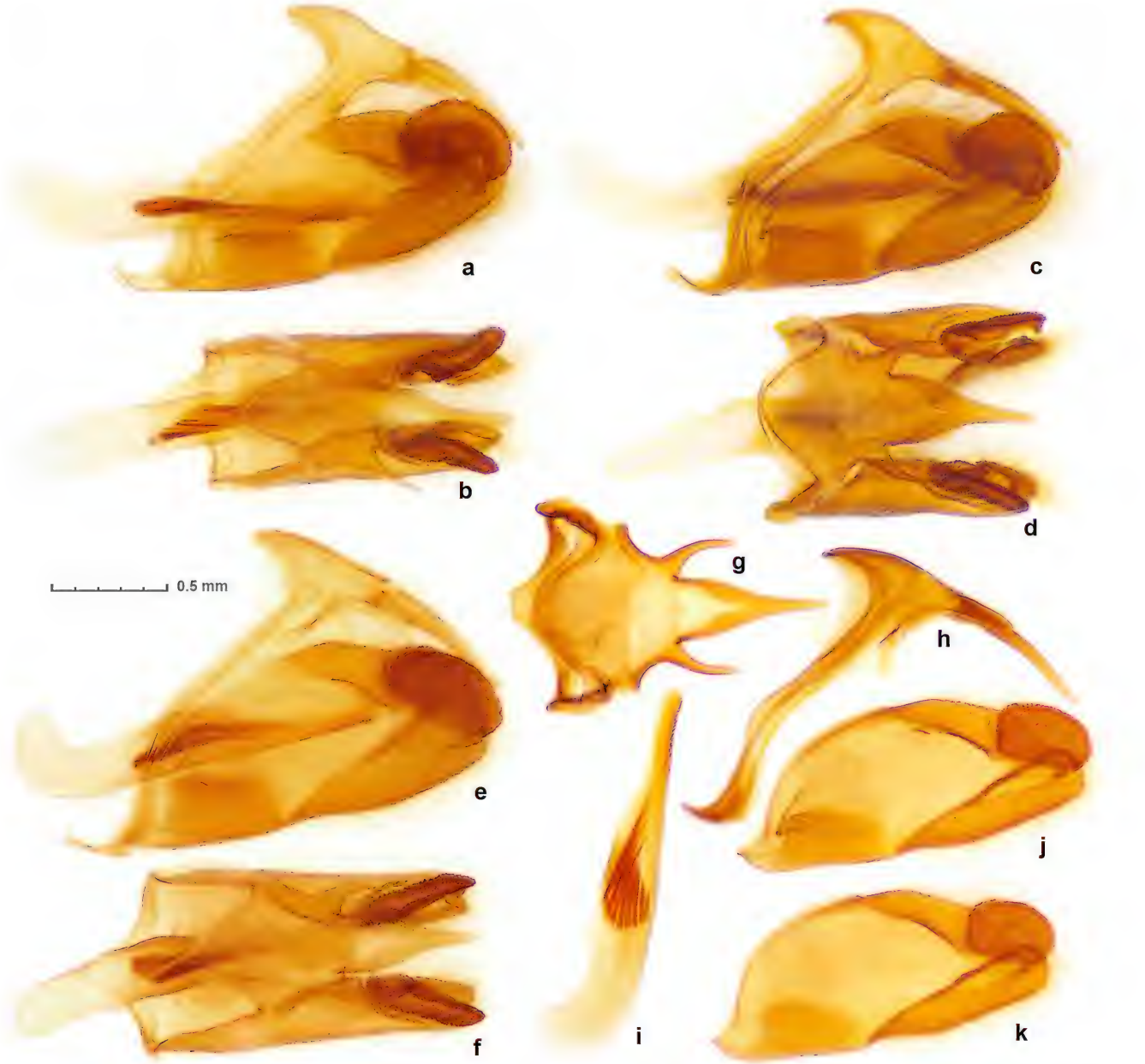


Fig. 103. Male genitalia of *Perus* (*Perus*), data in text or below: **a–d)** *P.* (*P.*) *perus* **sp. n.**: **a–b)** holotype NVG-7826 and **c–d)** paratype NVG-18058H06 and **e–k)** *P.* (*P.*) *cordillerae* from Ecuador, Loja [MGCL]: **e–f)** NVG-25014A09 Vilcabamba, 1600 m, May-1974, R. de Lafebre leg., vial SRS-2023 and **g–k)** NVG-24065A08 km 28 of Loja–Catamayo Rd., 1700 m, 11-Sep-1975, S. S. Nicolay leg., vial SRS-1979 in **a, c, e, h–k)** left lateral and **b, d, f, g)** dorsal views: **a–f)** complete genitalia and **g–h)** genitalia with **i)** aedeagus and **j)** left and **k)** right valvae detached and shown separately.

Type material. Holotype: ♂ currently deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 102a (genitalia in Fig. 103a, b), bears the following five printed rectangular labels, four white: [PERU, AM, 3 km | S Abra Chanchillo | 06° 49'S, 77° 57'W | 19.ix.99, 2150m | Robbins, Lamas, Ahrenholz], [DNA sample ID: | NVG-7826 | c/o Nick V. Grishin], [genitalia | NVG170206-11 | Nick V. Grishin], [USNMENT | {QR Code} | 01321666], and one red [HOLOTYPE ♂ | Perus (Perus) | perus Grishin]. Fringes of the holotype are rather evenly damaged, giving it a somewhat unusual appearance. **Paratypes:** 2♂♂ and 1♀ from Peru, La Libertad Region, Angasmarca, old [USNM]: 1♂ NVG-18058H06 (leg DNA extraction, sequenced), NVG-23121C11 (abdomen DNA extraction and dissection), USNMENT 01466752, genitalia NVG240817-74 (Figs. 102b, 103c, d); 1♂ NVG-23121F02; and 1♀ NVG-23121E12.

Type locality. Peru: Amazonas, 3 km south of Abra Chanchillo, elevation 2150 m, GPS −6.817, −77.950.

Etymology. For this new species from Peru, the name is tautonymous with the genus name and is treated as a masculine noun in apposition.

Distribution. Currently known from the Andean region in northern Peru.

Gomalia jeanneli levana Benyamini, 1990, comb. nov.

Genomic analysis of *Gomalia* F. Moore, 1879 (type species *Gomalia albofasciata* F. Moore, 1879) specimens reveals that *Gomalia jeanneli* (Picard, 1949) (type locality in Kenya, holotype sequenced as NVG-18079B11) is sister to *Gomalia albofasciata* Moore, 1879 (type locality in Sri Lanka) (Fig. 104), COI barcode difference of 2.3% (15 bp), and is more distantly related to *Gomalia elma* (Trimen, 1862) (type locality in South Africa) with which it is likely sympatric in Kenya, COI barcode difference of 6.4% (42 bp). Moreover, *Gomalia elma levana* Benyamini, 1990 (type locality in Israel) clusters closely with *G. jeanneli* and not with *G. elma*, not being strongly differentiated genetically from the former (Fig. 104); e.g., their COI barcodes differ by 0.9% (6 bp). Therefore, not having sufficient evidence to treat *G. elma levana* as a species-level taxon, we place it as a subspecies of *G. jeanneli*, instead of *G. elma* as originally proposed, to form a **new** species-subspecies combination: *Gomalia jeanneli levana* Benyamini, 1990.

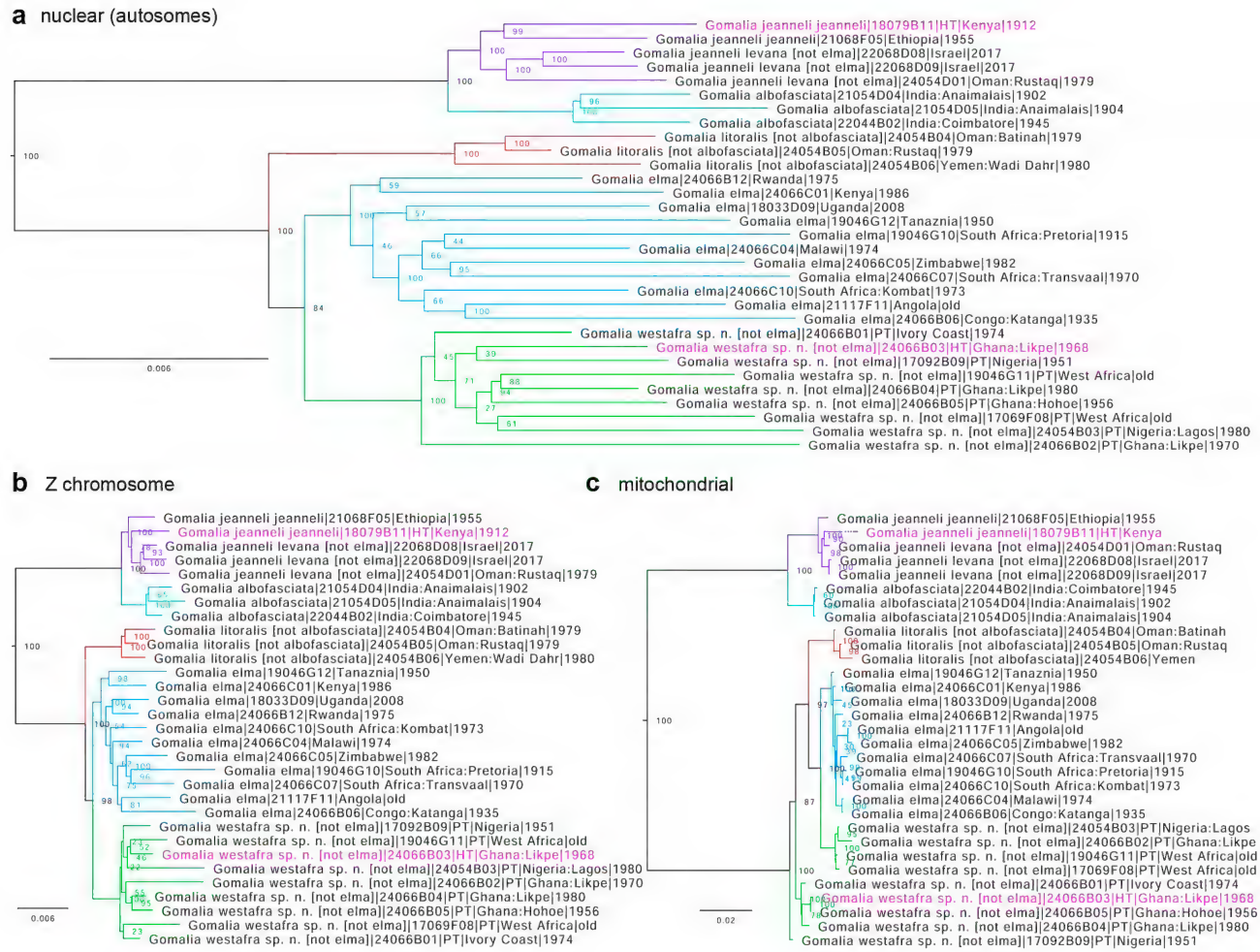


Fig. 104. Phylogenetic trees of *Gomalia* inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,176,192 positions, **b)** the Z chromosome, based on 116,643 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Primary types are labeled in red-purple. Different species are colored differently: *G. jeanneli* (purple), *G. albofasciata* (cyan), *G. litoralis* **stat. rest.** (red), *G. elma* (blue), and *G. westafra* **sp. n.** (green).

Thus far, we have only sequenced two specimens of *G. jeanneli*: the holotype from Kenya (see fig. 3 in Zhang et al. (2020a)) and another specimen from Ethiopia (Fig. 105a). Both specimens are males, are dark brown without the pale pattern characteristic of *Gomalia*, and are smaller than *G. elma* (Fig. 106c, d), similar in size to *G. jeanneli levana* (Fig. 105b). It is unclear whether all nominate *G. jeanneli* are small and brown like this, or if it is just a color form, and pale-patterned specimens of larger size exist in these populations.

Gomalia litoralis Swinhoe, 1885, stat. rest. is a valid species distinct from *Gomalia albofasciata* F. Moore, 1879

Genomic analysis of *Gomalia* F. Moore, 1879 (type species *Gomalia albofasciata* F. Moore, 1879) specimens from Oman and Yemen reveals that they partition into two clades (Fig. 104). One male (NVG-24054D01, Oman, Rustaq, 5-Mar-1979, T. B. Larsen leg. [ZMUC], Fig. 105b) is placed with *Gomalia jeanneli levana* Benyamini, 1990 (type locality in Israel), is phenotypically similar to it in being ventrally pale with a diffuse cream band and small size, and we identify it as this subspecies. Other specimens (T. B. Larsen leg. in ZMUC from Oman: 1♂ NVG-24054B04 Al Batinah Region, Barka 4-Mar-1979, Fig. 105c and 1♀ NVG-24054B05 Rustaq, 5-Mar-1979, Fig. 105d, and 1♂ NVG-24054B06 Yemen, Wadi Dahr, N of Sana'a, 10-May-1980) are larger, with more extensive and better-defined cream bands, and are in the clade with *Gomalia elma* (Trimen, 1862) (type locality in South Africa) (Fig. 106c, d), thus being more distant from *G. albofasciata* (type locality in Sri Lanka) (Fig. 105e) and *Gomalia jeanneli* (Picard, 1949) (type locality in Kenya) (Fig. 105a), and are genetically differentiated from them all at the species level (Fig. 104), e.g., their COI barcodes differ by 1.7% (11 bp) from *G. elma* and by 5.6% (37 bp) from *G. albofasciata*. Therefore, these specimens represent a distinct species that we identified as *Gomalia litoralis* Swinhoe, 1885 (type locality Pakistan: Karachi), which is currently treated as a junior subjective synonym of *G. albofasciata*. Therefore, we propose that *Gomalia litoralis* Swinhoe, 1885, **stat. rest.** is a valid species distinct from *Gomalia albofasciata* F. Moore, 1879.

Gomalia westafra Grishin, new species

http://zoobank.org/88CD5D4F-C4D4-4D29-8724-D379F4654CC9

(Figs. 104 part, 106a–b, 107a)

Definition and diagnosis. Genomic analysis of *Gomalia* F. Moore, 1879 (type species *Gomalia albofasciata* F. Moore, 1879) reveals that specimens from western Africa form a separate clade in the nuclear genome genetically differentiated from others at the species level (Fig. 104); e.g., their COI barcodes differ by about 1.8% (12 bp) from *Gomalia elma* (Trimen, 1862) (type locality in South Africa), by 1.7% (11 bp) from *Gomalia litoralis* Swinhoe, 1885 **stat. rest.** (type locality Pakistan: Karachi) and by 6.2% (41 bp) from *Gomalia albofasciata* Moore, 1879 (type locality in Sri Lanka), and, therefore, represent a new species. In the mitochondrial genome, the new species forms several separate clades, each containing only specimens of this species. This new species keys to "*Gomalia elma*" (III.A.(b^1)) in (Evans 1937) but differs from it and other relatives by the following combination of characters: tufts of hair-like scales by male genitalia are dark brown; wings are more rounded, darker and less variegated, as especially noticeable on the ventral side; cream hindwing band is narrower and better defined, with darker veins separating it into spots, the spot in the cell CuA_1-CuA_2 typically overlaps less with the spots between veins M_1 and CuA_1, and stronger sticks out basad from the band; harpe is more robust, with a more convex ventroposterior margin in lateral view; dorsal margin of sacculus is straighter, without a prominent concavity. Due to the partly cryptic nature of this species and poorly explored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly728.34.6:G33A, aly728.34.6:T69C, aly216.22.9:C33T, aly216.22.9: C69T, aly2661.9.1:C126T; and COI barcode: A43A, 88T, 424T, C483C, T553C, 646T.

Fig. 105. Specimens of *Gomalia* in dorsal (left) and ventral (right) views, additional data in text. **a)** *G. jeanneli jeanneli* ♂ NVG-21068F05 Ethiopia, Harari or Oromia Region, Erer River, 20-Aug-1955, S. Chojnacki leg. [MGCL], **b)** *G. jeanneli levana* ♂ NVG-24054D01, **c–d)** *G. litoralis* **stat. rest.** from Oman: **c)** ♂ NVG-24054B04 and **d)** ♀ NVG-24054B05, **e)** *G. albofasciata* ♂ NVG-22044B02 India, "Coimbatore Prov." [Tamil Nadu], 9-Nov-1945, P. Susai Nathan leg. [CUIC].

Fig. 106. Specimens of *Gomalia* in dorsal (left) and ventral (right) views, additional data are in text. *Gomalia westafra* **sp. n.**: **a)** holotype ♂ NVG-24066B03, **b)** paratype ♀ NVG-24054B03 and *G. elma* from South Africa: **c)** ♂ NVG-24066C07, UF FLMNH MGCL 1162207, "Transvaal Pienaar's River" [Limpopo Province, Pienaarsrivier], ~1970, Wm. Henning leg., genitalia NVG241111-28 (Fig. 107b) [MGCL], **d)** ♀ NVG-19046G10 Pretoria, 6-Mar-1915 [AMNH].

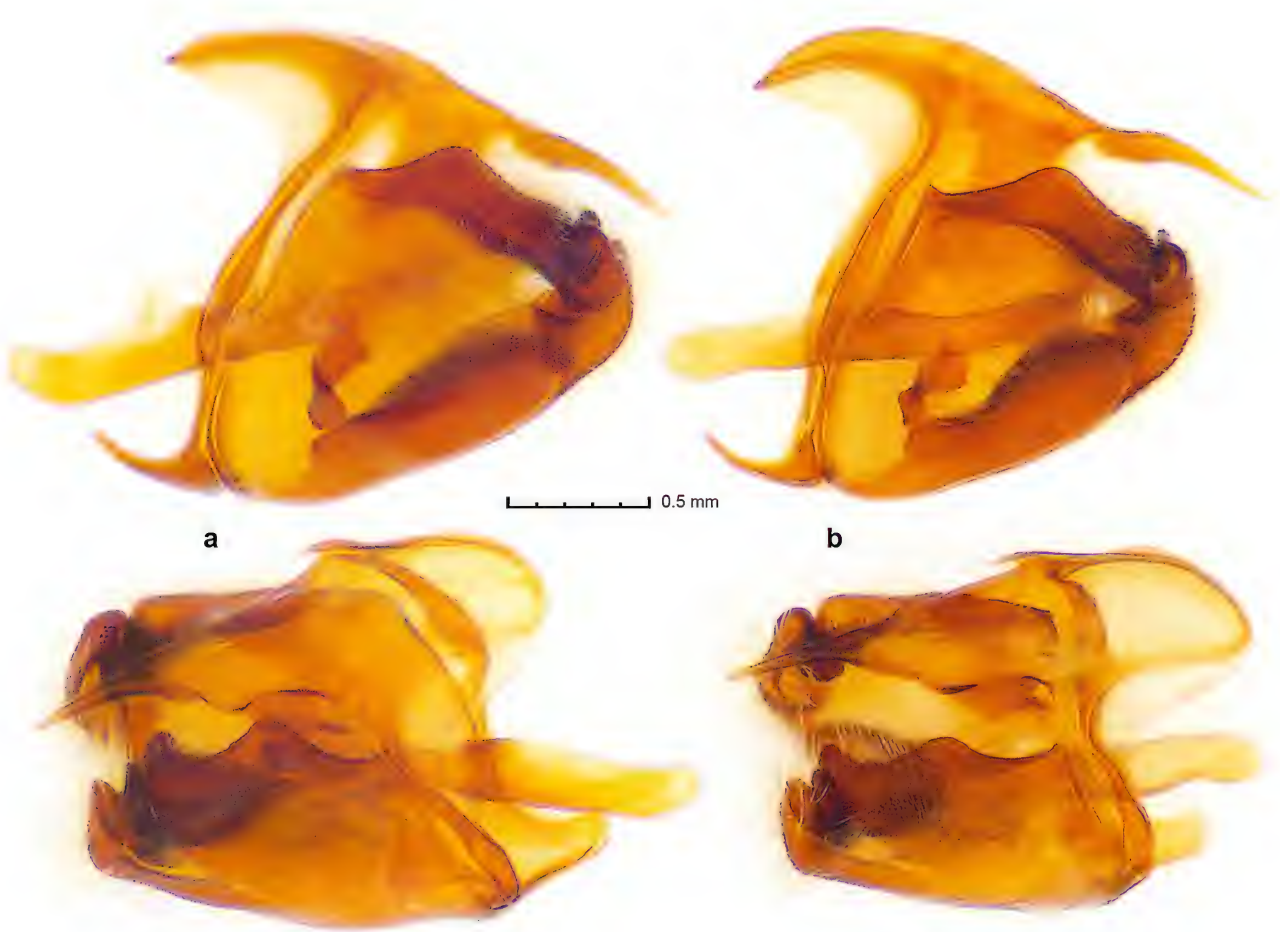


Fig. 107. Male genitalia of *Gomalia* in left lateral (above) and right dorsolateral (below, emphasizing the difference between species in the costa-ampulla area) views: **a)** *G. westafra* **sp. n.** paratype NVG-24066B02 (data in text), and **b)** *G. elma* NVG-24066C07 (specimen Fig. 106c, data in its legend).

Barcode sequence of the holotype. Sample NVG-24066B03, GenBank PV550047, 658 base pairs:

AACATTATATTTTATTTTTGGAATCTGATCAGGAATAGTAGGAACATCTTTAAGATTACTTATTCGATCAGAATTAGGAACACCTGGTTCACTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTCATTATAATTTTCTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCATCTCTTACTCTCTTAATTTCAAGTAGTATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTATCCTCCTCTCTCAGCTAATATTGC
CCACCAAGGATCTTCAGTAGATTTAGCTATCTTTTCCCTTCATTTAGCTGGAATTTCATCTATTTTAGGGGCAATTAATTTTATTACAACAATTATTAATATACGAGTTAATAATTTATCT
TTTGATCAAATACCTCTTTTTGTTTGAGCTGTTGGAATTACAGCTTTACTTTTATTATTATCTTTACCCGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 106a, bears the following five printed (text in italics handwritten) rectangular labels (3rd green, 5th red, others white) [GHANA | Likpe | *22-xi-1968* | Fr. Th. Maessen], [A. C. Allyn | Acc. 1969-6], [{QR Code} UF | FLMNH | MGCL 1162140], [DNA sample ID: | NVG-24066B03 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Gomalia westafra | Grishin]. **Paratypes:** 4♂♂ and 4♀♀: 1♂ NVG-24066B01, UF FLMNH MGCL 1162125 Côte d'Ivoire, Bouake, 25-Mar-1974, E. Munroe leg. [MGCL]; Ghana, the same data as the holotype except as specified: 1♂ NVG-24066B02, UF FLMNH MGCL 1162130, 6-Jul-1970, genitalia NVG241111-27 (Fig. 107a); 1♀ NVG-24066B04, UF FLMNH MGCL 1162146, 7-May-1980; and 1♀ NVG-24066B05, UF FLMNH MGCL 1162148 Hohoe instead of Likpe, 1-Jul-1956; Nigeria: 1♂ NVG-17092B09, USNMENT 00894593 Oyo State, Ibadan, May-Jun-1951, H. J. Sutton leg. [USNM] and 1♀ NVG-24054B03 Nigeria, Lagos State, Isheri, 5-Oct-1980, H. Kapala leg. [ZMUC]; and West Africa (no detailed locality, old specimens): 1♂ NVG-19046G11, AMNH_IZC 00346646 [AMNH] and 1♀ NVG-17069F08, USNMENT 00894397 [USNM].

Type locality. Ghana: Oti Region, Likpe.

Etymology. The name is given for the West African distribution of this species and is a feminine noun in apposition.

Distribution. Western Africa, currently known from Côte d'Ivoire, Ghana, and Nigeria.

Tribe Pyrgini Burmeister, 1878

Lectotype designation for *Carterocephalus biseriatus* Weymer, 1890

Carterocephalus biseriatus Weymer, 1890 was described from two specimens from the high plateau in Bolivia and illustrated in the original description as reproduced here in Fig. 108a (Weymer and Maassen 1890). Evans (1953) synonymized this name with *Hesperia* (*Syrichthus* [sic]) *limbata* Erschoff, 1876, the type of and currently a valid species in the genus *Chirgus* Grishin, 2019. We located and sequenced a syntype (labeled as "Lectotypus", although this designation was not published) (Fig. 108b) and a specimen identified as *C. biseriatus* placed next to the syntype in the drawer (Fig. 108c). Phylogenetic trees constructed from protein-coding genes in the nuclear genomes revealed that the two specimens were

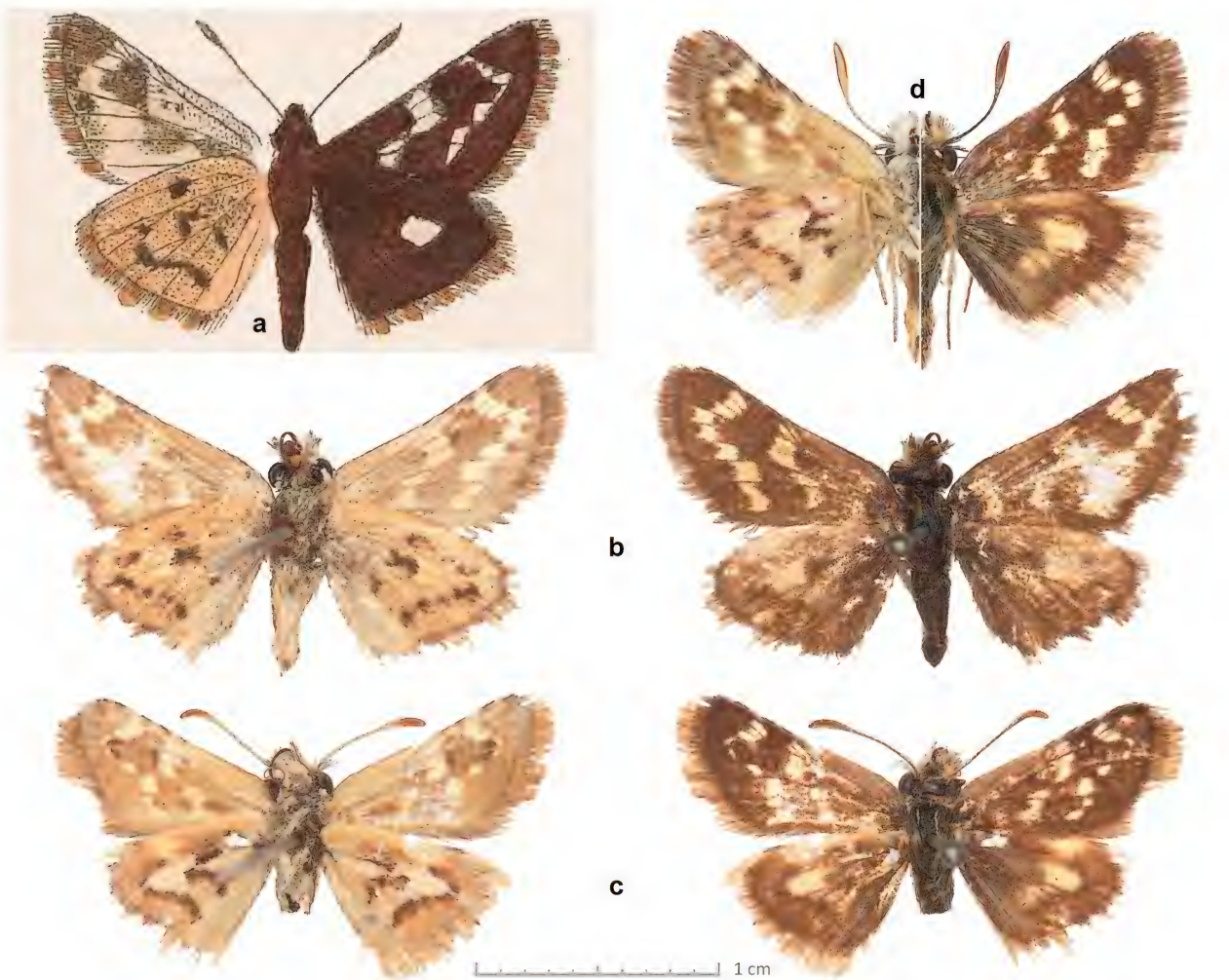


Fig. 108. *Chirgus biseriatus* and relatives in dorsal (right) and ventral (left) views: **a)** illustration of *Carterocephalus biseriatus* from Weymer and Maassen (1890); **b)** the lectotype of *C. biseriatus* designated herein, NVG-15033H08, data in text; **c)** a specimen of *Chirgus nigella* (NVG-15033H09) identified as *C. biseriatus* and placed next to the lectotype in the drawer; **d)** a specimen of *Chirgus biseriatus* **stat. rest.** from Peru: Arequipa Region, ca. 30 km NE of El Misti, 4100 m, 12-Oct-1983, E. S. Nielsen leg., NVG-22013C01 [RMNH]. All *Chirgus* specimens (Figs. 108, 110, 112, 114) are shown at the same scale to facilitate comparisons.

not conspecific (Fig. 109). The syntype was grouped with the specimens of *Chirgus barrosi* (Ureta, 1956) (type locality in Chile), and the other specimen was placed among *Chirgus nigella* (Weeks, 1902) (type locality in Bolivia). Phenotypic inspection agreed with this conclusion, and differing ventral wing patterns of the specimens were consistent with such placement (Fig. 108b, d vs. c). Evans's (1953) decision to synonymize *Carterocephalus biseriatus* with *C. limbata* instead of *C. nigella* was probably due to the original description and illustration (Evans did not have a chance to inspect the syntype) indicating a single pale spot on the brown ground color of the dorsal hindwing (more consistent with *C. limbata*) (Fig. 108a), while both the syntype and the other specimen exhibit more extensive pale patterns (more characteristic of *C. nigella*) (Fig. 108b, c).

The other specimen, although being from the Maassen collection and identified as *C. biseriatus*, is not likely to be a syntype because it has antennae intact, but the original description states that both syntypes lacked the antennae (Weymer and Maassen 1890). Moreover, judging from the handwriting, the identification label placed on this specimen was written by a different person, possibly by Mabille (after publication of the name), while the identification label on the syntype may have been written by Weymer, based on the handwriting on these labels. Conversely, the syntype we found agrees well with the original description and illustration of *C. biseriatus*. It is even possible that the ventral side illustration shows the right wings of this syntype: the hindwing has two rows of spots (3 and 5 spots), uniformly ochre-yellow otherwise, and the forewing is paler in the discal area than typical for this species. The artist might have mistaken the scale damage on this forewing for the pattern and illustrated a broader pale band instead of a narrow band of smaller pale spots. The dorsal side illustration is not particularly similar to this syntype: it is darker with much smaller pale spots and only one central spot on the hindwing. It might have depicted the second syntype (possibly not even conspecific with the first one), which we could not locate.

Fig. 109. Phylogenetic trees of *Chirgus* (*Chirgus)* constructed from protein-coding regions in: **a)** autosomes, **b)** the Z chromosome, and **c)** the mitochondrial genome. Primary type specimens are labeled in red. Branches corresponding to different species are colored in different colors: *C. biseriatus* (purple), *C. nigella* (cyan), *C. limbata* (green), *C argentinus* **sp. n.** (orange), *C. trisignatus* (blue), *C. teres* **sp. n.** (red), *C. sombrus* **sp. n.** (magenta), and *C. bocchoris* (aquamarine).

To stabilize nomenclature and define the name *C. biseriatus* objectively, N.V.G. hereby designates a syntype we found in the MFNB collection (shown in Fig. 108b) with the following eight rectangular labels (1st red, others white): [Lectotypus], [3083], [Coll. | Stübel], [Tacora], [Bolivien | Hochplateau | 3600-4600 m.], [Carterocephalus biseriatus Weym], [{QR Code} http://coll.mfn-berlin.de/u/ | 80a6f2], and [DNA sample ID: | NVG-15033H08 | c/o Nick V. Grishin] as the **lectotype** of *Carterocephalus biseriatus* Weymer, 1890. The lectotype has scales rubbed off on both sides in the discal area of the right forewing, a feature even depicted in the original illustration of the ventral side (Weymer & Maassen, 1890: pl. 4, fig. 7). Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15033H08, GenBank PV550048, 658 base pairs, is:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCATTAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCCTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGTGGATTCGGAAATTGATTAGTACCATTAATACTAGGAGCTCCAGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGATTATTACCTCCTTCATTAACATTACTTATTTCAAGTAGTATTGTAGAAAATGGTGCAGGAACTGGATGAACAGTTTACCCCCCTCTTTCAGCTAATATTGC
CCATCAAGGTTCTTCTGTTGATTTAGCTATTTTCTCTTTACATTTAGCAGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCCTTACTTCTTTTATTATCATTGCCTGTTTTAGCAGGAGCTATTACAATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Chirgus (*Chirgus*) *biseriatus* (Weymer, 1890) is a species distinct from *Chirgus* (*Chirgus*) *limbata* (Erschoff, 1876)

Genomic analysis of the lectotype of *Carterocephalus biseriatus* Weymer, 1890 (type locality in Bolivia, sequenced as NVG-15033H08) reveals that it belongs to a different clade than *Chirgus limbata* (Erschoff, 1876) (type locality in Peru), is confidently placed as sister to *Chirgus nigella* (Weeks, 1902) (type locality in Bolivia) in the Z chromosome tree, and is genetically differentiated from them at the species level (Fig. 109), e.g., the COI barcodes of *C. biseriatus* and *C. nigella* differ by 2.3% (15 bp). Therefore, we propose that *Chirgus (Chirgus) biseriatus* (Weymer, 1890), **stat. rest.** is a species distinct from *Chirgus* (*Chirgus*) *limbata* (Erschoff, 1876).

Pyrgus barrosi Ureta, 1956 is a subspecies of *Chirgus* (*Chirgus*) *biseriatus* (Weymer, 1890)

Genomic phylogeny that includes several specimens of *Chirgus biseriatus* (Weymer, 1890) (type locality in Bolivia, lectotype sequenced as NVG-15033H08, brown ground color of dorsal hindwing) and *Chirgus barrosi* (Ureta, 1956) (type locality in Chile, several topotypical paratypes sequenced, cream and nearly unmarked dorsal hindwing) reveals the lack of separation between them in nuclear genomes, although the mitochondrial genomes partition them into different clades (Fig. 109). Due to the lack of nuclear genomic differentiation, we propose to treat these two taxa as subspecies with the junior name being *Chirgus* (*Chirgus*) *biseriatus barrosi* Ureta, 1956, **stat. nov**. In summary, we show that *C. biseriatus* is not a synonym of *C. limbata*, but a species previously known as *C. barrosi*, which, due to wing pattern differences and separate geographic ranges, becomes a subspecies.

Chirgus (*Chirgus*) *argentinus* Grishin, new species

http://zoobank.org/6D8855C3-80A6-4F0F-8461-517F01A8427A

(Figs. 109 part, 110–111)

Definition and diagnosis. A specimen from Argentina initially identified as *Chirgus limbata* (Erschoff, 1876) (type locality in Peru) (Fig. 109 orange) is genetically differentiated from it at the species level in the nuclear genome (Fig. 109a, b), e.g., the F_{st} for their comparison is 0.24, and is not monophyletic with it in the mitochondrial genome tree (Fig. 109c), which is riddled with introgression. Therefore, this specimen represents a new species. This new species keys to "*Pyrgus limbata limbata*" (G.1.2.(a)) in Evans (1953) but differs from its relatives by a combination of the following characters: the pale spot in the middle of the dorsal hindwing discal cell is either absent or vestigial and the discal band (sometimes reduced to a central spot) is separated from the paler costal area, which may be vestigial; the ventral hindwing is paler and with a more contrasting dark pattern on it consisting of two bands (sometimes

broken into segments or spots) and a basal dark dot, the submarginal area distad of the postdiscal band is only slightly darker than the area between the two bands, without paler dots inside (usually darker in *C. limbata*, and may be with paler dots between veins); fringes are typically stronger checkered than in *C. limbata*. Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly525.91.4:A76T, aly525.91.4:A78T, aly1196.3.1:C306T, aly1196.3.1:T327C, aly587.15.1:C265T, aly619.10.5:G90G (not A), aly102.6.2:G543G (not A), aly102.6.2:C549C (not T), aly208.16.7:A24A (not T), aly208.16.7:G48G (not A). In the COI barcode, this species may not differ from some specimens of its relatives due to introgression.

Barcode sequence of the holotype. Sample NVG-15092G11, GenBank PV550049, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCATTAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCCTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGTGGATTCGGGAATTGATTAGTACCATTAATACTAGGAGCTCCAGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGATTATTACCTCCTTCATTAACATTACTTATTTCAAGTAGTATTGTAGAAAATGGTGCAGGAACTGGATGAACAGTTTACCCCCCTCTTTCAGCTAATATTGC
CCATCAAGGTTCTTCTGTTGATTTAGCTATTTTCTCTTTACATTTAGCAGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCCTTACTTCTTTTATTATCATTGCCTGTTTTAGCAGGAGCTATTACAATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 110 (genitalia Fig. 111), bears the following seven rectangular labels (2 handwritten, others printed), six white: [ARGENTINA Jujuy | (Tumbaya) | Purmamarca to Rt. | 40, Rt 52 km 38, | 4170 m 21-i-88 Leg | R Eisele 88J5], [♂], [MGCL Accession | #2011-4 | Robert Eisele], [DNA sample ID: | NVG-15092G11 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24068C09 | c/o Nick V. Grishin], [genitalia: | NVG241111-32 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Chirgus (Chirgus) | argentinus Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratype:** 1♀ NVG-24068C08 Argentina, Jujuy, Tilcara Department, Cerro Sisilera, 15 km SE of Huacalera, 4550 m, 20-Dec-1990, David Greenman leg. [MGCL].

Type locality. Argentina: Jujuy Province, Tumbaya Department, Purmamarca to Rt. 40, km 38 of Rt. 52, elevation 4170 m.

Fig. 110. *Chirgus* (*Chirgus*) *argentinus* **sp. n.** holotype ♂ NVG-15092G11 in dorsal (left) and ventral (right) views.

Fig. 111. Male genitalia of *Chirgus argentinus* **sp. n.** holotype NVG-15092G11 in left lateral (left) and dorsal (right) views.

Etymology. The name refers to the country with the type locality and is treated as a noun in apposition.
Distribution. Argentina.
Comment. Published records of *Chirgus limbata* from Argentina (Gomariz 2020; Núñez-Bustos 2023) likely refer to this species.

Chirgus (*Chirgus*) *trisignatus* (Mabille, 1875) is a species distinct from *Chirgus* (*Chirgus*) *bocchoris* (Hewitson, 1874)

Genomic phylogeny reveals that in all three trees *Scelothrix* [sic] *trisignatus* Mabille, 1875 (type locality Chile: Valparaiso), currently treated as a subspecies of *Chirgus* (*Chirgus*) *bocchoris* (Hewitson, 1874) (type locality in Bolivia) (Fig. 109 aquamarine), is strongly differentiated from it genetically (Fig. 109 blue), forming a distinct clade that includes specimens throughout the range. The Z chromosome F_{st} of the two taxa is 0.44, their COI barcodes differ by 1.4% (9 bp), and they possess distinct wing patterns as detailed by Evans (1953). Therefore, we propose that *Chirgus* (*Chirgus*) *trisignatus* (Mabille, 1875), **stat. rest.** is a species distinct from *Chirgus* (*Chirgus*) *bocchoris* (Hewitson, 1874).

Hesperia (*Battus*) *cuzcona* Draudt, 1923 is confirmed as a subspecies of *Chirgus* (*Chirgus*) *bocchoris* (Hewitson, 1874), but is frequently misidentified

Genomic analysis of the lectotype of *Hesperia* (*Battus*) *cuzcona* Draudt, 1923 (type locality in Peru: Cuzco, sequenced as NVG-18093A12) places it within specimens of *Chirgus* (*Chirgus*) *bocchoris bocchoris* (Hewitson, 1874) (type locality in Bolivia) and away from several specimens from Cuzco in Peru that we identified as "*Chirgus bocchoris cuzcona*" using Evans (1953) (Fig. 109). Neither the Z chromosome (Fig. 109b) nor the mitochondrial DNA trees (Fig. 109c) reveal overall genetic differentiation between *H. cuzcona* lectotype and *C. bocchoris bocchoris*, suggesting that they are conspecific. However, the nuclear genome tree places the lectotype as sister to all other sequenced specimens of *C. bocchoris bocchoris* (none from Peru), implying some genetic uniqueness of Peruvian populations. Therefore, we propose to keep *Hesperia* (*Battus*) *cuzcona* Draudt, 1923, as a subspecies of *Chirgus* (*Chirgus*) *bocchoris* (Hewitson, 1874) pending further research. Curiously, the original description (English version) of *H. cuzcona* states: "wings … above the white spots are a little more prominent … the spot of the hindwing oblong quadrangular" (Draudt 1923), consistently with the wing pattern of the lectotype (Fig. 109) and the wing pattern of *C. bocchoris*, but contrary to how *H. cuzcona* was described (and consequently misidentified) later: "Uph more or less unmarked" (Evans 1953). Specimens from the Andes of Peru with unmarked hindwings that Evans (1953) misidentified as "*Pyrgus bocchoris cuzcona*" represent two new species that are described next.

Chirgus (*Chirgus*) *teres* Grishin, new species

http://zoobank.org/9214666A-C343-4E07-ADAE-E5792AA61A1F

(Figs. 109 part, 112–113)

Definition and diagnosis. As demonstrated above, *Chirgus* (*Chirgus*) *bocchoris cuzcona* Draudt, 1923 (type locality in Peru: Cuzco, lectotype sequenced as NVG-18093A12) is genetically and phenotypically similar to *Chirgus* (*Chirgus*) *bocchoris bocchoris* (Hewitson, 1874) (type locality in Bolivia) rather than to specimens that are traditionally identified as *C. bocchoris cuzcona* in collections. Genomic analysis of such specimens reveals that they are genetically differentiated from *C. bocchoris* at the species level and form two clades representing two new species (Fig. 109). The first new species is from the Andes in Central Peru. It differs from *C. bocchoris* with F_{st}/G_{min} of 0.48/0.016. Evans (1953) misidentified this species as "*Pyrgus bocchoris cuzcona*" (in part), thus it keys to (G.1.4b) in Evans (1953). It differs from its relatives by a more weakly defined and overscaled with brown central spot on the dorsal hindwing, the lack of mottling on the ventral side with smooth and more connected dark bands on the hindwing, and less distinctly checkered fringes. Due to unexplored individual variation, most reliable identification is

achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly6286.6.4:T90A, aly164.59.1:A149C, aly164.59.1:A189C, aly331.12.22:A54G, aly331.12.22:A111T. This species does not differ in COI barcodes from *C. bocchoris* or a new species described next. It differs, however, in the overall mitochondrial DNA (Fig. 109c).

Barcode sequence of the holotype. Sample NVG-23058C10, GenBank PV550050, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCATTAAGTTTATTAATTCGAACTGAATTAGGAAACCCAGGATCATTAATTGGAGATGATCAAATTTATAATACC
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCCCCAGACATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGATTATTACCCCCCTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAATGGTGCTGGAACTGGATGAACAGTTTACCCCCCTCTCTCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTCTCTTTACATTTAGCAGGTATTTCATCAATTTTAGGAGCTATTAATTTTATCACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCTTTACTTCTTTTATTATCACTTCCTGTTTTAGCAGGAGCTATTACAATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 112 (genitalia Fig. 113), bears the following six printed rectangular labels, five white: [12km NNE La Oroya | 4100-4150m | JuninPERU | Jack L. Harry | 14Oct2005], [MGCL Acc. | #2015-47 | J. L. Harry] [DNA sample ID: | NVG-23058C10 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24067E11 | c/o Nick V. Grishin], [genitalia: | NVG241111-31 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Chirgus (Chirgus) | teres Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratypes:** 2♂♂ in Ernst Brockmann collection: NVG-15083E03 from the type locality, 2000 and NVG-15083E02 from Peru, Pasco Region, C. de Pasco, 4000 m, 2001.

Type locality. Peru: Junín Region, 12 km north-northeast of La Oroya, elevation 4100–4150 m.

Etymology. In Latin, *teres* means smooth or round, highlighting a curved form with a smooth surface. The name reflects the ventral hindwing pattern of smoother and rounder curves and smoother, not variegated, overscaling compared to the closest relatives of this species. The name is an adjective.

Distribution. The Andes of central Peru.

Fig. 112. *Chirgus* (*Chirgus*) *teres* **sp. n.** holotype ♂ NVG-23058C10 in dorsal (left) and ventral (right) views, data in text.

Fig. 113. Male genitalia of *Chirgus* (*Chirgus*) *teres* **sp. n.** holotype NVG-23058C10 in left lateral (left) and dorsal (right) views.

Chirgus (*Chirgus*) *sombrus* Grishin, new species

http://zoobank.org/B729E05D-7B8C-4283-9E32-47EF5892A115

(Figs. 109 part, 114–115)

Definition and diagnosis. As demonstrated above, *Chirgus* (*Chirgus*) *bocchoris cuzcona* Draudt, 1923 (type locality in Peru: Cuzco, lectotype sequenced as NVG-18093A12) is genetically and phenotypically similar to *Chirgus* (*Chirgus*) *bocchoris bocchoris* (Hewitson, 1874) (type locality in Bolivia) rather than to specimens that are traditionally identified as *C. bocchoris cuzcona* in collections. Genomic analysis of such specimens reveals that they are genetically differentiated from *C. bocchoris* at the species level and form two clades representing two new species (Fig. 109). The first new species is described above. The second new species is from the Andes in Southern Peru. It differs from the first new species and *C. bocchoris* with F_{st}/G_{min} of 0.55/0.006 and 0.35/0.035, respectively. Evans (1953) misidentified this species as "*Pyrgus bocchoris cuzcona*" (in part), thus it keys to (G.1.4b) in Evans (1953). It differs from its relatives by a more weakly defined and strongly overscaled with brown central spot on the dorsal hindwing and mottled ventral side, with more angular dark bands on the hindwing mostly separated into spots; fringes are prominently checkered, but mainly in the basal half on the hindwing (the entire hindwing fringe is uniformly checkered in *C. bocchoris*). Due to unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly887.8.7:A450G, aly887.8.7:A3153T, aly887.8.7:A3222G, aly2379.20.1:G484T, aly2379.22.10:C147T. This species does not differ in COI barcodes from *C. bocchoris* or *C. teres* **sp. n.** described above. It differs, however, in the overall mitochondrial DNA (Fig. 109c).

Fig. 114. *Chirgus* (*Chirgus*) *sombrus* **sp. n.** holotype ♂ NVG-23058C12 in dorsal (left) and ventral (right) views, data in text.

Fig. 115. Male genitalia of *Chirgus sombrus* **sp. n.** paratype NVG-17069B06 in left lateral (left) and dorsal (right) views.

Barcode sequence of the holotype. Sample NVG-23058C12, GenBank PV550051, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCATTAAGTTTATTAATTCGAACTGAATTAGGAAACCCAGGATCATTAATTGGAGATGATCAAATTTATAATACC
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCCCCAGACATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGATTATTACCCCCCTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAATGGTGCTGGAACTGGATGAACAGTTTACCCCCCTCTCTCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTCTCTTTACATTTAGCAGGTATTTCATCAATTTTAGGAGCTATTAATTTTATCACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCTTTACTTCTTTTATTATCACTTCCTGTTTTAGCAGGAGCTATTACAATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCAGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 114, bears the following four printed (text in italics handwritten) rectangular labels, three white: [Ayaviri 4050m | Colquejaua | PunoPERU | Jack L. Harry | 30Oct2005], [MGCL Acc. | #2015-47 | J. L. Harry], [DNA sample ID: | NVG-23058C12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Chirgus (Chirgus) | sombrus Grishin]. **Paratypes:** 3♂♂ and 1♀: 2♂♂ from the type locality: NVG-24068C10 the same data as the holotype [MGCL] and NVG-17069B06 (leg DNA extraction, sequenced), NVG-23119F10 (abdomen DNA extraction and dissection), USNMENT 01321973, James H. Baker collection, 14-Feb-1970, genitalia vial NVG240817-61 (Fig. 115) [USNM]; and from Peru, Cuzco, R. F., B. D. Denno, M. J. Raupp leg. [MGCL]: 1♂ NVG-15092G03 9 km N of Cuzco, Ruinas Tambomachay, 3500 m, 10-Feb-1980 and 1♀ NVG-15092G04 (leg DNA extraction), NVG-24067E10 (abdomen DNA extraction and dissection), 6 km N of Cuzco, Ruinas Qenqo, 3-Mar-1980, genitalia vial NVG241111-30.

Type locality. Peru: Puno Region, Melgar Province, Ayaviri, elevation 4050 m.

Etymology. In Spanish, sombra means shadow, given for the darker dorsal hindwing with a "shaded" central white patch that identifies this species. The name is treated as a masculine noun in apposition.

Distribution. The Andes of southern Peru.

Comment. This species was previously referred to by the name *Pyrgus bocchoris cuzcona* (Draudt, 1923) (or *Chirgus bocchoris cuzcona*), a misidentification.

Zopyrion (*Zopyrion*) *thyas* Evans, 1953 is a species distinct from *Zopyrion* (*Zopyrion*) *subvariegata* Hayward, 1942

Genomic analysis of a topotype of *Zopyrion subvariegata thyas* Evans, 1953 (type locality in Peru: Amazonas, Chachapoyas), together with another specimen from Cajamarca, Peru, reveals that they are genetically differentiated from *Zopyrion subvariegata subvariegata* Hayward, 1942 (type locality in Ecuador) at the species level (Fig. 116); e.g., their COI barcodes differ by 5.3% (35 bp). Therefore, we propose that *Zopyrion* (*Zopyrion*) *thyas* Evans, 1953, **stat. nov.** is a species distinct from *Zopyrion* (*Zopyrion*) *subvariegata* Hayward, 1942.

Lectotype designation for *Zopyrion sandace* Godman & Salvin, 1896

Zopyrion sandace Godman & Salvin, 1896 was described from a series of specimens from several places in Guerrero, Mexico, and one specimen from Guatemala (Godman and Salvin 1896). To stabilize nomenclature, clarify the type locality, and define the name *Z. sandace* objectively, N.V.G. hereby designates a syntype in the BMNH collection that, according to its label, was illustrated by Godman and Salvin (1896), and bears the following eleven labels (first three and the last round, others rectangular; first three with a red circle, last yellow, others white; 7th and the last handwritten, others printed): (Type), (Type), (Type) and on the other side of this label handwritten (H | 876), [R. Papagaio, | Guerrero, 1200ft. | Oct. H.H.Smith.], [Sp. figured.], [♂], [Zopyrion | sandace, sp.n | Type Figd.], [B.C.A.Lep.Rhop. | Zopyrion | sandace, | G.&S.], [Godman-Salvin | Coll. 1912.—23.], [ ] genitalia are glued to this label without text, (966) as the **lectotype** of *Zopyrion sandace* Godman & Salvin, 1896. The lectotype has the costal fold open on the right forewing and closed on the left forewing, wings are glued to the body, and a patch of scales is missing at the base of the left hindwing above (likely due to removal of a dried glue patch). Images of this specimen are shown on the Butterflies of America website

(Warren et al. 2024). The type locality of *Z. sandace* becomes Mexico: Guerrero, Río Papagayo, elevation 1200 ft.

Zopyrion (*Zopyrion*) *xerxes* Grishin, new species

http://zoobank.org/7B0DD951-B5E8-49AD-8A50-B6F772AD4F3E

(Figs. 116 part, 117, 118a–c)

Definition and diagnosis. Genomic analysis reveals that a specimen from Honduras identified as *Zopyrion sandace* Godman & Salvin, 1896 (type locality in Mexico: Guerrero) is genetically differentiated from it at the species level (Fig. 116); e.g., their COI barcodes differ by 2.6% (17 bp). Therefore, this specimen represents a new species. This new species is similar to *Z. sandace* and keys to it (E.58.1) in Evans (1953). The new species differs from its relatives by typically being paler and somewhat warmer colored, with better marked dorsal side of wings, including both a submarginal row of darker spots and postdiscal row of paler spots (with subapical ones); by a smaller harpe, gradually narrowing towards the end (Fig. 118a, c), not terminally rounded as in *Z. sandace* (Fig. 118d, f), and by a less robust, narrower long process of the ampulla with the smaller inner lobe (Fig. 118b vs. e). Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved

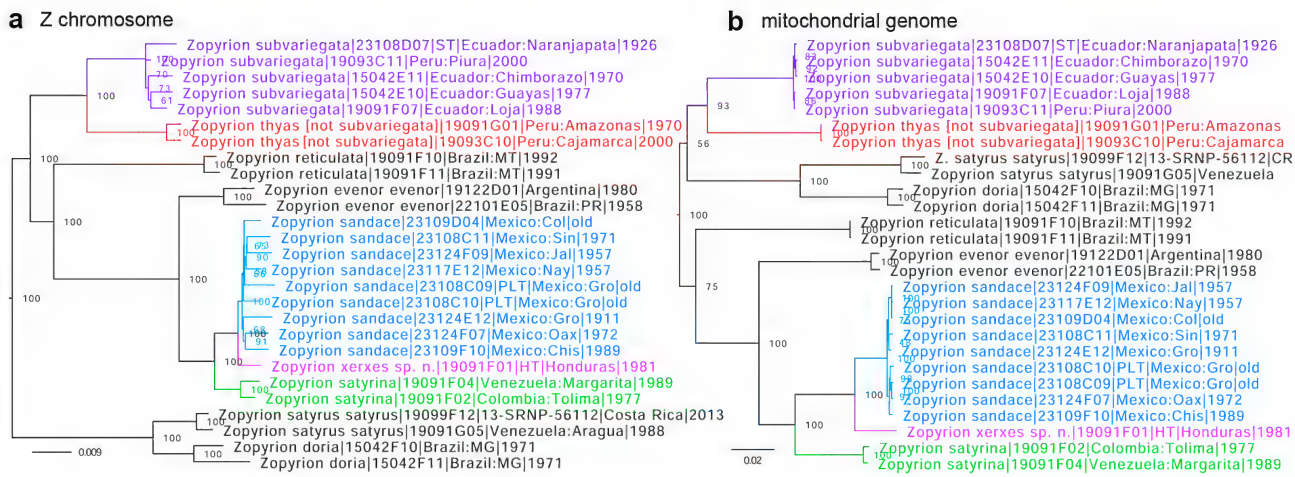


Fig. 116. Phylogenetic trees of *Zopyrion* species constructed from protein-coding regions in: **a)** the Z chromosome, based on 190,077 positions, and **b)** the mitochondrial genome: *Z. subvariegata* (purple), *Zopyrion thyas* **stat. nov.** (red), *Z. sandace* (blue), *Z. xerxes* **sp. n.** (magenta), and *Z. satyrina* (C. Felder & R. Felder, 1867) (green). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

Fig. 117. *Zopyrion* (*Zopyrion*) *xerxes* **sp. n.** holotype ♂ NVG-19091F01 in dorsal (left) and ventral (right) views, data in text.

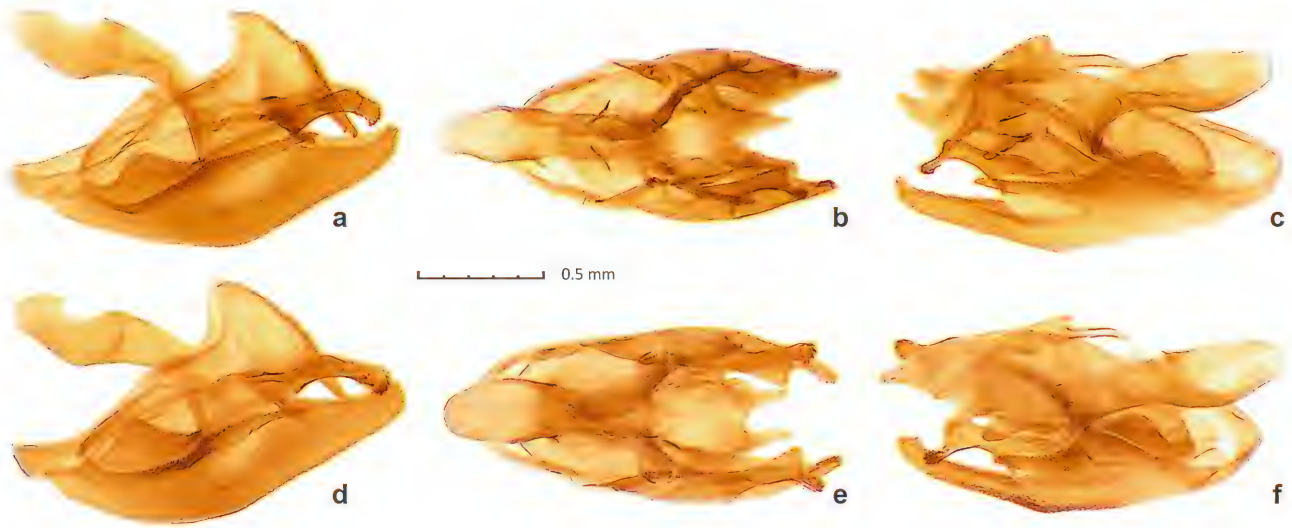


Fig. 118. Male genitalia of *Zopyrion* (*Zopyrion*): **a–c)** *Z.* (*Z.*) *xerxes* **sp. n.** holotype NVG-19091F01, vial no. X-4380 J.M. Burns 1998 and **d–f)** *Z.* (*Z.*) *sandace* NVG-23124F07, vial no. X-4379 J.M. Burns 1998, Mexico, Oaxaca, 65 mi SE of Oaxaca, 15-Aug-1972, G. F. & S. Hevel leg. [USNM] in different views: **a**, **d)** left lateral, **b**, **e)** dorsal, and **c**, **f)** right dorsolateral.

by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1041.25.4:A39T, aly322.41.23:G57A, aly14.4.12:G108A, aly1259.43.1:A48C, aly216.2.1:A148G, aly2012.17.2:T252T (not C), aly116.38.4:G1132G (not T), aly1689.9.8:G117G (not A), aly88.7.2:C82C (not A), aly84.9.4:C198C (not T); and COI barcode: A28A, A184T, C367C, 401T, T514C, A550G.

Barcode sequence of the holotype. Sample NVG-19091F01, GenBank PV550052, 658 base pairs:

AACTTTATACTTCATTTTTGGAATTTGAGCAGGAATAGTTGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCTCTAATTGGAGATGATCAAATTTATAATACT
ATCGTAACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGTTTTGGAAATTGATTAGTACCATTAATACTTGGGGCCCCAGATATAGCTTTCCCCCGTA
TAAATAATATAAGATTTTGATTATTGCCCCCTTCATTAACATTATTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAACAGGATGAACAGTTTACCCCCCCCTTTCAGCTAACATTGC
TCACCAAGGTTCTTCTGTTGATTTAGCAATTTTTTCCTTACATTTAGCAGGTATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAGAAATTTATCT
TTTGATCAAATACCTTTATTTGTATGAGCCGTAGGAATTACAGCTTTACTTTTATTATTATCACTGCCTGTATTAGCAGGAGCTATTACTATACTTTTAACTGATCGAAATTTAAATACAT
CTTTTTTTGATCCAGCTGGAGGAGGAGATCCTATTCTTTATCAACACTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 177 (genitalia Fig. 118a–c), bears the following four rectangular labels (1st handwritten, others printed with handwritten text shown in italics), three white: [San Pedro Sula, | Honduras | 4-VII-1981 | Robert O. Lehman], [GENITALIA NO. | X-*43 80* | J.M.Burns 199*8*], [DNA sample ID: | NVG-19091F01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Zopyrion (Zopyrion) | xerxes Grishin].

Type locality. Honduras: San Pedro Sula.

Etymology. Sandace was the sister of Xerxes I, a king of the Achaemenid Empire of Persia who ruled from 486 to 465 BC. It seems fitting to use the name *xerxes* for this new species whose sister was named *sandace*. The name is a masculine noun in apposition.

Distribution. Currently known only from the holotype collected in Honduras.

Anisochoria bacchoides Grishin, new species

http://zoobank.org/C3887697-B08C-4BD4-9A8B-B2E76F59D016

(Figs. 119 part, 120–121)

Definition and diagnosis. Genomic sequencing of several specimens from El Salvador and Chiapas, Mexico, reveals that they are genetically differentiated from *Anisochoria bacchus* Evans, 1953 (type locality Mexico: Veracruz, Atoyac) at the species level (Fig. 119); e.g., their COI barcodes differ from *A. bacchus* by 2.9% (19 bp). Therefore, these specimens represent a new species. This new species keys to "*Anisochoria pedaliodina bacchus*" (E.59.1.(a)) in Evans (1953) and was included within this taxon.

However, it differs from its sister species *A. bacchus* by the following combination of characters: three subapical forewing spots are in a straighter line nearly at a right angle with the costa, the line drawn through them from the costal spot is directed towards the tornus rather than towards the spot in cell M_3-CuA_1; spots in cell M_3-CuA_1 and the lower spot in the discal cell are farther apart from each other than in *A. bacchus*; spots in the discal cell are usually smaller in size; and the process of the ampulla is longer compared to the harpe. Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly85.36.7: A81G, aly528.11.7:C43T, aly3512.6.1:T144C, aly3512.6.1:A165T, aly3512.6.1:G214A; and COI barcode: T50C, T112C, A160G, 274C, T463C, T539C.

Barcode sequence of the holotype. Sample NVG-23054D06, GenBank PV550053, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCACTAAGTTTATTAATTCGAACTGAATTAGGAAATCCAGGATCTTTAATTGGAGATGATCAAATCTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATGGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTGGTACCTTTAATGTTAGGGGCACCCGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTTTGATTATTACCCCCCTCTTTAACATTATTAATTTCTAGAAGTATTGTAGAAAATGGAGCAGGAACTGGATGAACAGTTTATCCCCCCCTTTCATCTAATATCGC
TCATCAAGGATCTTCTGTAGATTTAGCTATTTTCTCCCTTCACTTAGCTGGAATTTCATCAATTTTAGGAGCTATTAATTTCATTACTACAATTATTAACATACGAATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTCTGAGCTGTAGGAATTACTGCTATTCTTTTACTATTATCTTTACCTGTATTAGCTGGAGCTATTACTATATTATTAACAGATCGAAATTTAAACACAT
CTTTTTTTGACCCTGCTGGAGGTGGGGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 120, bears the following five printed (text in italics handwritten) rectangular labels, four white: [La Libertad, El Sal. | 10m. | *15-XII-72* | No. *H-6039* | Leg S.&L.Steinhauser], [*ANISOCHORIA PEDALIODINA* | *BACCHUS Ev.* ♂ | Det: S.R.Steinhauser], [A. C. Allyn | Acc. 1973-23], [DNA sample ID: | NVG-23054D06 | c/o Nick V. Grishin], and one red

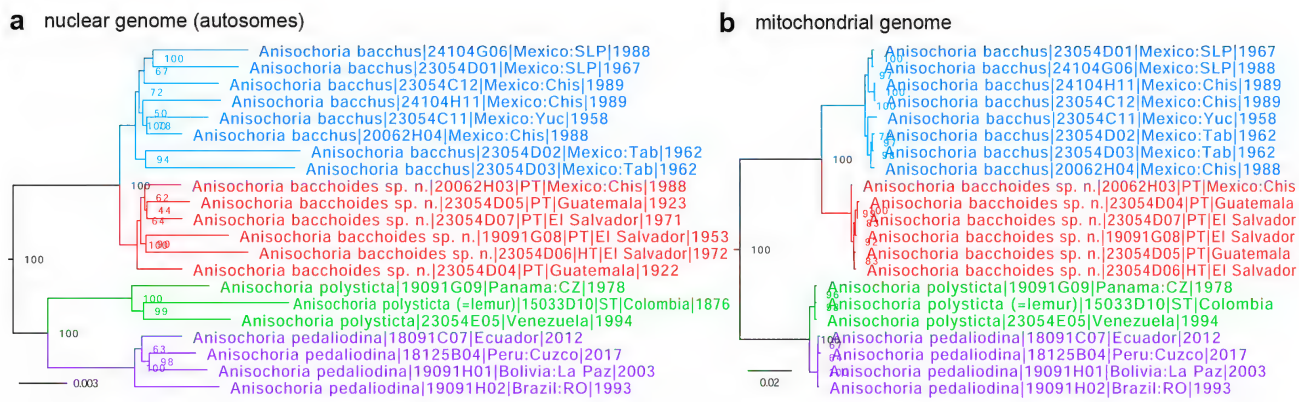


Fig. 119. Phylogenetic trees of selected *Anisochoria* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,278,153 positions, and **b)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species are colored differently: *A. bacchus* (blue), *A. bacchoides* **sp. n.** (red), *A. polysticta* Mabille, 1877 (green), and *A. pedaliodina* (A. Butler, 1870) (purple).

Fig. 120. *Anisochoria bacchoides* **sp. n.** holotype ♂ NVG-23054D06 in dorsal (left) and ventral (right) views, data in text.

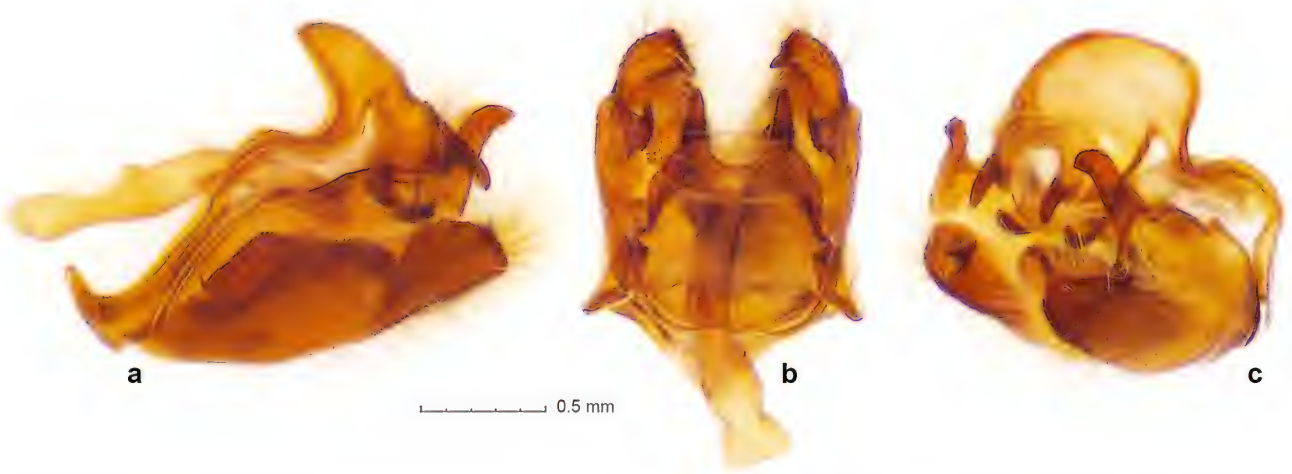


Fig. 121. Male genitalia of *Anisochoria bacchoides* **sp. n.** paratype NVG-20062H03 in **a)** left lateral, **b)** dorsal, and **c)** right posterolateral views.

[HOLOTYPE ♂ | Anisochoria | bacchoides Grishin]. **Paratypes:** 2♂♂ and 3♀♀: 1♂ NVG-20062H03 (leg DNA extraction, sequenced), NVG-24015E07 (abdomen DNA extraction and dissection) Mexico, Chiapas, Tuzantán, Rio Huixtla 7 mi N of Huixtla, 7-Aug-1988, J. Kemner leg., genitalia vial NVG241114-13 (Fig. 121) [TMMC]; Guatemala, Santa Rosa, Guazacapán, ex coll. E. Le Moult [MGCL]: 1♂ NVG-23054D04 5-Apr-1922 and 1♀ NVG-23054D05 1-Mar-1923; and El Salvador: 1♀ NVG-19091G08 Santa Tecla, 19-Dec-1953, Mauricio Salazar leg. [USNM] and 1♀ NVG-23054D07 Rio El Molino, nr. Ahuachapán, S. and L. Steinhauser leg. [MGCL].

Type locality. El Salvador: La Libertad, elevation 10 m.

Etymology. The name is formed from the name of its sister species, *A. bacchus*, made longer for this more southern relative. The name is treated as a feminine noun in apposition.

Distribution. Currently known from southern Chiapas (Mexico), Guatemala, and El Salvador.

Tribe Erynnini Brues & F. Carpenter, 1932

The COI barcode of the holotype of *Timochares fuscifasciata* Grishin, 2024

Instead of the holotype, the COI barcode sequence of a paratype was given in the original description of *Timochares fuscifasciata* Grishin, 2024, because the holotype has not been sequenced yet. Since then, it has been sampled, its whole genome shotgun dataset obtained, and the following label added to the

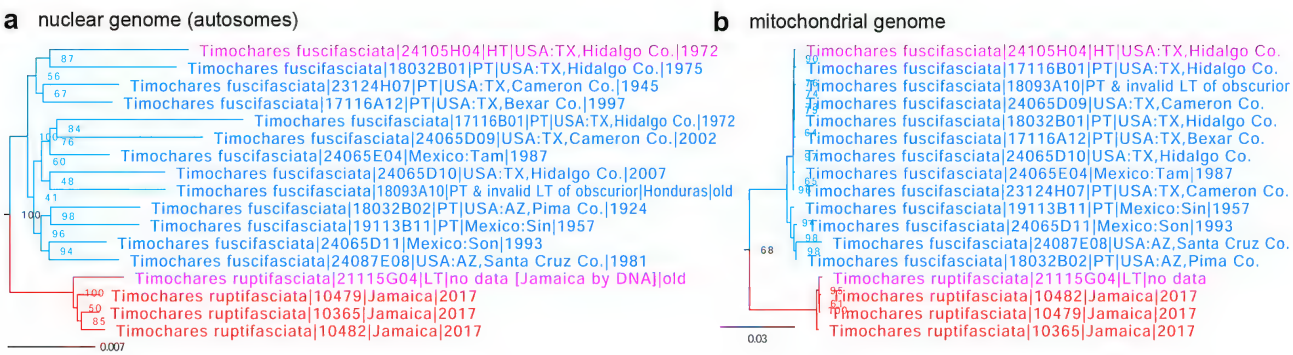


Fig. 122. Phylogenetic trees of *Timochares fuscifasciata* (blue) and *Timochares ruptifasciata* (red) inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 1,302,732 positions, and **b)** the mitochondrial genome. Primary type specimens are labeled in magenta.

holotype: [DNA sample ID: | NVG-24105H04 | c/o Nick V. Grishin]. Additional specimens of this species were also sequenced (Fig. 122). The COI barcode sequence of the holotype, sample NVG-24105H04, GenBank PV550054, 658 base pairs, is identical to the one reported for the paratype in the original description and is:

AACTTTATACTTTATTTTTGGAATTTGGGCAGGAATAGTTGGAACTTCTCTAAGTCTTCTTATTCGAACTGAATTAGGAAATCCCGGATCCTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTCATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCATTAATATTAGGAGCCCCAGATATAGCATTTCCACGAA
TAAATAATATAAGATTTTGACTTTTACCCCCCTCTTTAATATTATTAATTTCTAGAAGAATCGTAGAAAATGGAGCCGGAACAGGATGAACAGTTTATCCCCCCCTTTCAGCTAATATTGC
ACATCAAGGTTCTTCTGTAGACTTAGCTATTTTTTCCCTACATTTAGCAGGTATTTCCTCAATTCTTGGAGCAATTAACTTTATTACAACAATTATTAATATGCGAATTAGAAATTTATCT
TTTGACCAAATACCTTTATTTGTTTGAGCTGTTGGTATTACAGCATTACTTTTGTTATTATCTTTACCAGTTTTAGCTGGAGCTATTACTATACTTTTAACTGACCGAAATCTTAATACAT
CATTTTTTGACCCTGCGGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Subfamily Hesperiinae Latreille, 1809
Tribe Hesperiini Latreille, 1809

Onespa gala (Godman, 1900) and *Onespa brockorum* Austin & A. Warren, 2009 lack overall genetic differentiation typical of species-level taxa

Genomic analysis of *Onespa* Steinhauser, 1974 (type species *Onespa nubis* Steinhauser, 1974) reveals a surprise (Fig. 123). Despite phenotypic differences in both sexes, including slight differences in genitalia between *Onespa brockorum* Austin & A. Warren, 2009 (type locality in Mexico: Sonora) and *Onespa gala* (Godman, 1900) (type locality in Mexico: Veracruz, holotype sequenced as NVG-18117F05) discussed by Austin and Warren (2009) (who nevertheless note "*Onespa brockorum* is very similar to *O. gala*"), we failed to find DNA differences between them typical of species-level taxa. The two species do not separate phylogenetically, i.e., they do not form prominent and strongly supported clades in any of the three trees: the nuclear genome (autosomes), the Z chromosome, and the mitochondrial genome. This is the first example we encountered when a pair of species with reported genitalic differences in both sexes (albeit rather minute in our opinion) do not form separate well-supported clades in the genomic trees, and it warrants a more detailed study. It is possible that the two taxa are subspecies (in genome-scale trees, valid subspecies do not always segregate into discrete clades), or they speciated only recently and have not gained sufficient overall genetic differentiation in the presence of reproductive isolation. Here, we bring this unusual example to the attention of the research community without proposing taxonomic changes to the current classification.

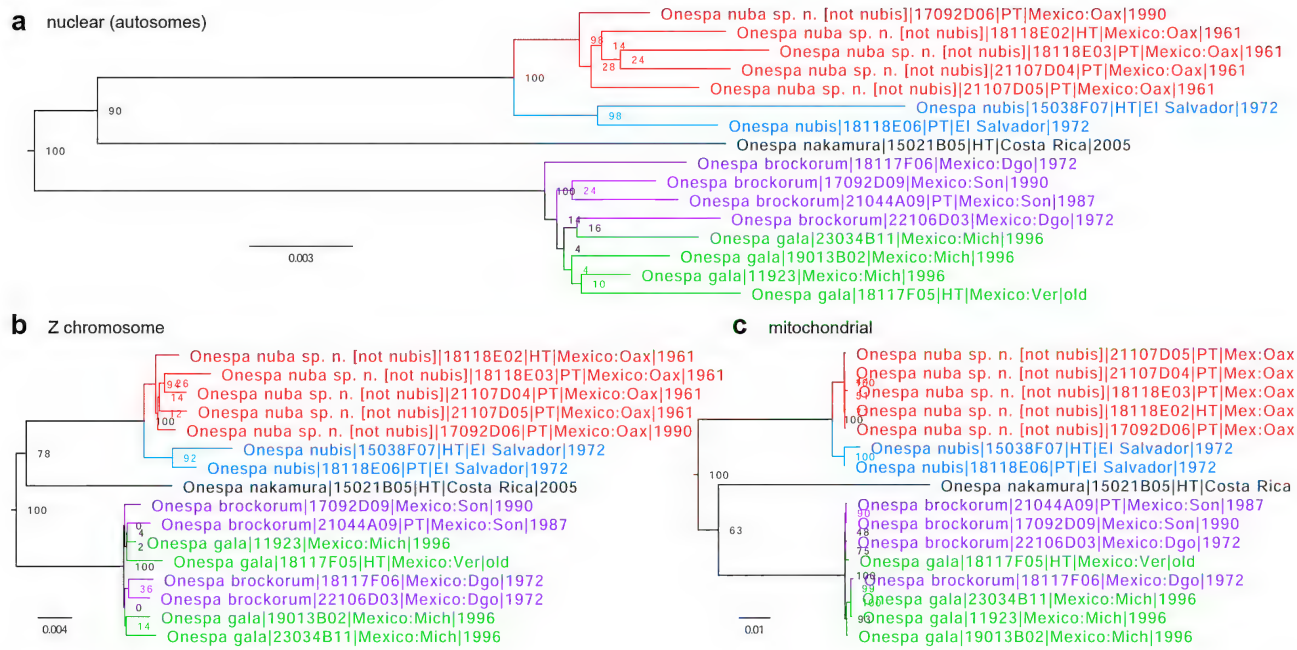


Fig. 123. Phylogenetic trees of *Onespa* species inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), **b)** the Z chromosome, and **c)** the mitochondrial genome. Different species are shown in different colors: *O. nuba* **sp. n.** (red), *O. nubis* (blue), *O. nakamura* Austin & A. Warren, 2009 (black), *O. brockorum* (purple), and *O. gala* (green).

Onespa nuba Grishin, new species

http://zoobank.org/B166E5B8-4E66-4798-9058-ABB3E797B5F7

(Figs. 123 part, 124–125)

Definition and diagnosis. In contrast to the lack of the overall genetic differentiation typical of species-level taxa between *Onespa brockorum* Austin & A. Warren, 2009 (type locality in Mexico: Sonora) and *Onespa gala* (Godman, 1900) (type locality in Mexico: Veracruz, holotype sequenced as NVG-18117F05) (see above), specimens currently within the concept of *Onespa nubis* Steinhauser, 1974 (type locality in El Salvador, holotype sequenced as NVG-15038F07) separate into two prominent clades: northern (from Oaxaca) and southern (from El Salvador) (Fig. 123). Specimens between the two clades are genetically differentiated at the species level, and their F_{st}/G_{min}/COI barcode differences are 0.24/0.017/1.1% (7 bp). Therefore, considering the lack of overall combined DNA-based distinction between *O. brockorum* and *O. gala*, the two "*nubis*" clades represent two distinct species, and the species from Oaxaca is new. This new species was previously included in the concept of *O. nubis* as detailed by Austin and Warren (2009). It differs from *O. nubis*, in both sexes, by generally smaller yellow spots (except the forewing discal cell spot that is usually larger) that are typically deeper yellow; weaker ochreous overscaling at the wing bases above (usually rather extensive in *O. nubis*, covering more than a posterior quarter of the hindwing from its base), e.g., in males, forewing costal cell is mostly orange above, more strongly contrasting with the darker color of the wing base due to the lack of extensive

Fig. 124. *Onespa nuba* **sp. n.** holotype ♂ NVG-18118E02 in dorsal (left) and ventral (right) views, data in text.

Fig. 125. Male genitalia of *Onespa nuba* **sp. n.** paratype NVG-21107D04, X-2855 (data in text) in different views: **a)** left and **b)** right lateral, **c)** dorsal, and **d)** posterolateral, in the plane of three cornuti.

ochreous overscaling; and redder rather than yellower hue of ventral ground color, e.g., at the forewing apex and most of the hindwing. Valva is narrower and is less expanded ventrad past the middle, but with a broader distal end of the harpe. Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly276558.35.1:T118C, aly276558.35.1:G405T, aly102.22.1:T336C, aly537.21.1:T168A, aly537.21.1: G228A; and COI barcode: T82T, C266T, A400A, T500C, A577A, T595C.

Barcode sequence of the holotype. Sample NVG-18118E02, GenBank PV550055, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACTTCTTTAAGTTTATTAATTCGTACAGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTCATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGAGCTCCTGACATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATATTACCCCCTTCATTAACCTTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCAGGAACAGGATGAACGGTTTACCCCCCCCTATCATCTAATATTGC
CCATCAAGGATCTTCTGTGGATTTAGCTATTTTTTCACTTCATTTAGCTGGTATTTCATCAATTTTAGGAGCTATTAATTTTATTACTACAATCATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATATCCCTATTTGTATGATCTGTAGGAATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATACTACTTACAGATCGAAACTTAAATACCT
CATTTTTTGACCCAGCAGGAGGAGGAGACCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), illustrated in Fig. 124, bears the following seven rectangular labels (1st handwritten, others printed with handwritten text shown in italics), six white: [Mo Coúo (Cerro | Pelón) Mpio. Yolox | Oaxaca, MEXICO | 2150 m. | E. C. Welling], [*13-IX-1961* | Collection of | Lee D. Miller], [L. & S. Miller | Coll. C.M.Acc. | 21269 & 21733], [GENITALIA NO. | X- *28 53* | J.M.Burns 199*0*], [Buzyges *nubis* | ♂ *(STEINHAUSER)* | det. J.M.Burns *1990*], [DNA sample ID: | NVG-18118E02 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Onespa nuba | Grishin]. **Paratypes:** 1♂ and 3♀♀ from Mexico, Oaxaca: 1♀ NVG-17092D06 3 mi S of Telea de Castro, 6000', 18-Aug-1990, John Kemner leg., genitalia X-3070 J.M.Burns 1991 [USNM] and others from the same locality, collector and collection as the holotype: 1♂ NVG-21107D04 12-Sep-1961, genitalia X-2855 J.M.Burns 1990 (Fig. 125) and 2♀♀ 13-Sep-1961: NVG-18118E03, genitalia X-2854 J.M.Burns 1990 and NVG-21107D05.

Type locality. Mexico: Oaxaca, Mpio. de San Pedro Yólox, Cerro Pelón, elevation 2150 m.

Etymology. In Spanish, nube means cloud. The name of the new species has the same root as the name of its close sister, *O. nubis* (Latin for cloud, mist, haze), but is made shorter for its more northern relative. The name is treated as a feminine noun in apposition.

Distribution. Currently known only from Oaxaca, Mexico.

Hesperia pahaska tehaska Grishin, new subspecies

http://zoobank.org/B60AB082-28E4-4B12-AA0F-FB84DBD5A043

(Figs. 126 part, 127, 128 part)

Definition and diagnosis. Genomic analysis reveals that southern populations currently identified as *Hesperia pahaska williamsi* Lindsey, 1940 (type locality in USA: Arizona, Pima Co.) form a clade that is distinct from it and are genetically differentiated from other populations at the subspecies level (Fig. 126); e.g., their COI barcodes differ by 0.8% (5 bp) from the genetically closest subspecies *H. p. williamsi*. Therefore, these populations represent a new subspecies. This new subspecies keys to "*Hesperia columbia pahaska*" (M.10.5.(b)) in Evans (1955) and statistically differs from other subspecies of *H. pahaska* Leussler, 1938 (type locality in USA: Nebraska, Sioux Co.) by a combination of the following characters: typically larger size, larger white spots on the ventral side of wings than in *H. pahaska williamsi*, ventrally darker and greener than *H. pahaska pahaska*, and typically with longer, better-defined subapical and submarginal spots on the dorsal forewing. Due to extensive individual variation and possibly cryptic nature of this subspecies, most reliable identification is achieved by DNA and a combination of the following base pairs is diagnostic in the nuclear genome: aly3598.2.1:C783T, aly3598. 2.1:G610A, aly383.17.7:C1131A, aly383.17.7:A1176T, aly479.9.3:G207A; and COI barcode: T19C, A373G, T386C, A562G, T613C.

Barcode sequence of the holotype. Sample NVG-23049B09, GenBank PV550058, 658 base pairs:

AACTTTATATTTTATTTTCGGTATTTGAGCTGGTATATTAGGAACTTCATTAAGTTTATTAATTCGAACAGAATTAGGTAATCCTGGATCTTTAATTGGAGATGACCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCACGTA
TAAATAATATAAGATTTTGAATATTACCACCTTCATTAACATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGATGAACTGTTTATCCTCCTTTATCCTCTAATATTGC
TCACCAAGGGTCTTCTGTTGATCTAGCAATTTTTTCTCTTCACTTAGCTGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAATTAAAAACTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGAATTACAGCATTATTATTACTTTTATCTTTACCTGTATTAGCGGGAGCTATTACTATACTACTTACTGACCGAAATTTAAATACTT
CTTTTTTCGATCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

a
nuclear
(autosomes)
Hesperia pahaska hannawackeri|22055G11|PT|USA:CO,Montrose Co.|2016
Hesperia pahaska hannawackeri|22055G10|PT|USA:CO,Delta Co.|1983
Hesperia pahaska hannawackeri|22055G09|PT|USA:CO,Mesa Co.|2007
Hesperia pahaska hannawackeri|22055G08|PT|USA:CO,Mesa Co.|2007
Hesperia pahaska hannawackeri|PAO566|PT|USA:CO,Mesa Co.|2017
Hesperia pahaska hannawackeri|20045F06|HT|USA:UT,San Juan Co.|2016
Hesperia pahaska hannawackeri|23049F06|USA:CO,Grand Co.|2000
Hesperia pahaska hannawackeri|23049E06|USA:CO,Garfield Co.|1968
Hesperia pahaska hannawackeri|23049C06|USA:UT,Uintah Co.|1968
Hesperia pahaska hannawackeri|23049C02|USA:UT,Garfield Co.|1972
Hesperia pahaska hannawackeri|23049C08|USA:UT,Wayne Co.|1979
Hesperia pahaska hannawackeri|22055G12|PT|USA:CO,Montrose Co.|2016
Hesperia pahaska hannawackeri|20045F09|HT|USA:UT,San Juan Co.|2020
Hesperia pahaska hannawackeri|23049C03|USA:UT,Grand Co.|1975
Hesperia pahaska hannawackeri|23051B09|USA:UT,Kane Co.|1988
Hesperia pahaska hannawackeri|23049C05|USA:UT,Kane Co.|1979
Hesperia pahaska hannawackeri|23051C09|USA:AZ,Coconino Co.|1950
Hesperia pahaska hannawackeri|23049D03|USA:NV,Lincoln Co.|1984
Hesperia pahaska hannawackeri|23051A03|USA:AZ,Navajo Co.|1982
Hesperia pahaska hannawackeri|23049C04|USA:UT,Grand Co.|1975
Hesperia pahaska hannawackeri|23049C07|USA:UT,San Juan Co.|1969
Hesperia pahaska hannawackeri|23049F04|USA:CO,San Miguel Co.|1971
Hesperia pahaska hannawackeri|23051C03|USA:UT,Emery Co.|1998
Hesperia pahaska hannawackeri|23051B10|USA:AZ,Coconino Co.|1987
Hesperia pahaska williamsi|23051C07|Mexico:Chih/Son|1985
Hesperia pahaska williamsi|23051C06|Mexico:Son|1986
Hesperia pahaska williamsi|23051C11|USA:AZ,Santa Cruz Co.|1988
Hesperia pahaska williamsi|23051B12|USA:AZ,Santa Cruz Co.|1995
Hesperia pahaska williamsi|23049G09|Mexico:Son|1984
Hesperia pahaska williamsi|23049G06|USA:AZ,Yavapai Co.|1965
Hesperia pahaska williamsi|23049C12|USA:AZ,Santa Cruz Co.|1980
Hesperia pahaska williamsi|23049C11|USA:AZ,Cochise Co.|1980
Hesperia pahaska williamsi|8279|USA:AZ,Pinal Co.|2017
Hesperia pahaska williamsi|20067B03|Mexico:Son|1998
Hesperia pahaska williamsi|23049D02|USA:AZ,Mohave Co.|1979
Hesperia pahaska williamsi|20067B02|Mexico:Son|2004
Hesperia pahaska williamsi|23049C09|USA:UT,Washington Co.|1955
Hesperia pahaska williamsi|15096B10|HT|USA:AZ,Pima Co.|1923
Hesperia pahaska williamsi|22047D12|PT|USA:AZ,Mohave Co.|old
Hesperia pahaska williamsi|23051B05|USA:AZ,Graham Co.|1963
Hesperia pahaska williamsi|23049H11|USA:AZ,Yavapai Co.|1980
Hesperia pahaska martini|23051B11|USA:NV,White Pine Co.|1969
Hesperia pahaska martini|23051C05|USA:NV,Clark Co.|1969
Hesperia pahaska martini|23049F11|USA:NV,Clark Co.|1969
Hesperia pahaska martini|23051A04|PT|USA:CA,San Bernardino Co.|1955
Hesperia pahaska martini|23049D10|PT|USA:CA,San Bernardino Co.|1955
Hesperia pahaska martini|21048F12|USA:CA,San Bernardino Co.|1981
Hesperia pahaska martini|20067B05|USA:CA,San Bernardino Co.|1959
Hesperia pahaska martini|15105D04|HT|USA:CA,San Bernardino Co.|1955
Hesperia pahaska martini|21048F11|USA:CA,San Bernardino Co.|1978
Hesperia pahaska martini|21048G01|USA:CA,San Bernardino Co.|1978
Hesperia pahaska tehaska ssp. n.|23049B04|PT|USA:TX,Presidio Co.|1973
Hesperia pahaska tehaska spp. n.|23051A01|PT|USA:TX,Brewster Co.|2008
Hesperia pahaska tehaska ssp. n.|23049B07|PT|USA:TX,Pecos Co.|1973
Hesperia pahaska tehaska ssp. n.|23051B03|PT|USA:TX,Culberson Co.|1973
Hesperia pahaska tehaska ssp. n.|23049B09|HT|USA:TX,Jeff Davis Co.|1977
Hesperia pahaska tehaska ssp. n.|11128|PT|USA:TX,Jeff Davis Co.|2018
Hesperia pahaska tehaska ssp. n.|23049B08|PT|USA:TX,Pecos Co.|1974
Hesperia pahaska tehaska ssp. n.|23049B10|PT|USA:TX,Jeff Davis Co.|1977
Hesperia pahaska tehaska ssp. n.|23049B05|PT|USA:TX,Presidio Co.|1961
Hesperia pahaska tehaska ssp. n.|23051B02|PT|USA:TX,Brewster Co.|1977
Hesperia pahaska tehaska ssp. n.|23051B01|PT|USA:TX,Brewster Co.|1974
Hesperia pahaska tehaska ssp. n.|10967|PT|USA:TX,Jeff Davis Co.|2018
Hesperia pahaska tehaska ssp. n.|23051C10|PT|USA:TX,McCulloch Co.|1980
Hesperia pahaska hidalgo ssp. n.|23049G08|HT|Mexico:Hgo|1981
Hesperia pahaska hidalgo ssp. n.|24097G03|PT|Mexico:Hgo|1981
Hesperia pahaska bajanorta ssp. n.|23049G10|HT|Mexico:BC Norte|1980
Hesperia pahaska bajanorta ssp. n.|23049G11|PT|Mexico:BC Norte|1980
Hesperia pahaska bajanorta ssp. n.|23049H01|PT|Mexico:BC Norte|1980
Hesperia pahaska bajanorta ssp. n.|23049G12|PT|Mexico:BC Norte|1980
Hesperia pahaska pahaska|21048F09|USA:NE,Sioux Co.|1985
Hesperia pahaska pahaska|22057C05|USA:NM,Lincoln Co.|2020
0.003
b
Z chromosome
Hesperia pahaska hannawackeri|23049D03|USA:NV,Lincoln Co.|1984
Hesperia pahaska hannawackeri|20045F05|PT|USA:UT,San Juan Co.|2020
Hesperia pahaska hannawackeri|22055G12|PT|USA:CO,Montrose Co.|2016
Hesperia pahaska hannawackeri|23049C08|USA:UT,Wayne Co.|1979
Hesperia pahaska hannawackeri|23049C04|USA:UT,Grand Co.|1975
Hesperia pahaska hannawackeri|20045F06|HT|USA:UT,San Juan Co.|2016
Hesperia pahaska hannawackeri|23051A03|USA:AZ,Navajo Co.|1982
Hesperia pahaska hannawackeri|23051B09|USA:UT,Kane Co.|1988
Hesperia pahaska hannawackeri|22055G08|PT|USA:CO,Mesa Co.|2007
Hesperia pahaska hannawackeri|PAO566|PT|USA:CO,Mesa Co.|2017
Hesperia pahaska hannawackeri|22055G09|PT|USA:CO,Mesa Co.|2007
Hesperia pahaska hannawackeri|22055G10|PT|USA:CO,Delta Co.|1983
Hesperia pahaska hannawackeri|23051C09|USA:AZ,Coconino Co.|1950
Hesperia pahaska hannawackeri|23051C03|USA:UT,Emery Co.|1998
Hesperia pahaska hannawackeri|22055G11|PT|USA:CO,Montrose Co.|2016
Hesperia pahaska hannawackeri|23049C03|USA:UT,Grand Co.|1975
Hesperia pahaska hannawackeri|23049C05|USA:UT,Kane Co.|1979
Hesperia pahaska hannawackeri|23049C07|USA:UT,San Juan Co.|1969
Hesperia pahaska hannawackeri|23049F06|USA:CO,Grand Co.|2000
Hesperia pahaska hannawackeri|23049E06|USA:CO,Garfield Co.|1968
Hesperia pahaska hannawackeri|23049C06|USA:UT,Uintah Co.|1968
Hesperia pahaska hannawackeri|23049C02|USA:UT,Garfield Co.|1972
Hesperia pahaska hannawackeri|23051B10|USA:AZ,Coconino Co.|1987
Hesperia pahaska hannawackeri|23049F04|USA:CO,San Miguel Co.|1971
Hesperia pahaska williamsi|22047D12|PT|USA:AZ,Mohave Co.|old
Hesperia pahaska williamsi|15096B10|HT|USA:AZ,Pima Co.|1923
Hesperia pahaska williamsi|23051C07|Mexico:Chih/Son|1985
Hesperia pahaska williamsi|23049G09|Mexico:Son|1984
Hesperia pahaska williamsi|23051C11|USA:AZ,Santa Cruz Co.|1988
Hesperia pahaska williamsi|23049C09|USA:UT,Washington Co.|1955
Hesperia pahaska williamsi|20067B02|Mexico:Son|2004
Hesperia pahaska williamsi|8279|USA:AZ,Pinal Co.|2017
Hesperia pahaska williamsi|20067B03|Mexico:Son|1998
Hesperia pahaska williamsi|23049G06|USA:AZ,Yavapai Co.|1965
Hesperia pahaska williamsi|23049D02|USA:AZ,Mohave Co.|1979
Hesperia pahaska williamsi|20067B04|Mexico:Son|2003
Hesperia pahaska williamsi|23051C01|USA:AZ,Gila Co.|1988
Hesperia pahaska williamsi|23049H11|USA:AZ,Yavapai Co.|1980
Hesperia pahaska williamsi|23051C06|Mexico:Son|1986
Hesperia pahaska williamsi|23051B12|USA:AZ,Santa Cruz Co.|1995
Hesperia pahaska williamsi|23049C11|USA:AZ,Cochise Co.|1980
Hesperia pahaska williamsi|23049C12|USA:AZ,Santa Cruz Co.|1980
Hesperia pahaska williamsi|23051B05|USA:AZ,Graham Co.|1963
Hesperia pahaska martini|23051B11|USA:NV,White Pine Co.|1969
Hesperia pahaska martini|15105D04|HT|USA:CA,San Bernardino Co.|1955
Hesperia pahaska martini|21048F11|USA:CA,San Bernardino Co.|1978
Hesperia pahaska martini|21048F12|USA:CA,San Bernardino Co.|1981
Hesperia pahaska martini|21048G01|USA:CA,San Bernardino Co.|1978
Hesperia pahaska martini|20067B05|USA:CA,San Bernardino Co.|1959
Hesperia pahaska martini|23051A04|PT|USA:CA,San Bernardino Co.|1955
Hesperia pahaska martini|23049D10|PT|USA:CA,San Bernardino Co.|1955
Hesperia pahaska martini|23049F11|USA:NV,Clark Co.|1969
Hesperia pahaska martini|23051C05|USA:NV,Clark Co.|1969
Hesperia pahaska tehaska ssp. n.|23049B07|PT|USA:TX,Pecos Co.|1973
Hesperia pahaska tehaska ssp. n.|11128|PT|USA:TX,Jeff Davis Co.|2018
Hesperia pahaska tehaska ssp. n.|23049B05|PT|USA:TX,Presidio Co.|1961
Hesperia pahaska tehaska ssp. n.|23049B10|PT|USA:TX,Jeff Davis Co.|1977
Hesperia pahaska tehaska ssp. n.|23051B02|PT|USA:TX,Brewster Co.|1977
Hesperia pahaska tehaska ssp. n.|23051C10|PT|USA:TX,McCulloch Co.|1980
Hesperia pahaska tehaska ssp. n.|23049B04|PT|USA:TX,Presidio Co.|1973
Hesperia pahaska tehaska ssp. n.|23049B09|HT|USA:TX,Jeff Davis Co.|1977
Hesperia pahaska tehaska ssp. n.|23051A01|PT|USA:TX,Brewster Co.|2008
Hesperia pahaska tehaska ssp. n.|23051B01|PT|USA:TX,Brewster Co.|1974
Hesperia pahaska tehaska ssp. n.|10967|PT|USA:TX,Jeff Davis Co.|2018
Hesperia pahaska tehaska ssp. n.|23049B08|PT|USA:TX,Pecos Co.|1974
Hesperia pahaska tehaska ssp. n.|23051B03|PT|USA:TX,Culberson Co.|1973
Hesperia pahaska hidalgo ssp. n.|23049G08|HT|Mexico:Hgo|1981
Hesperia pahaska hidalgo ssp. n.|24097G03|PT|Mexico:Hgo|1981
Hesperia pahaska bajanorta ssp. n.|23049G10|HT|Mexico:BC Norte|1980
Hesperia pahaska bajanorta ssp. n.|23049G12|PT|Mexico:BC Norte|1980
Hesperia pahaska bajanorta ssp. n.|23049G11|PT|Mexico:BC Norte|1980
Hesperia pahaska bajanorta ssp. n.|23049H01|PT|Mexico:BC Norte|1980
Hesperia pahaska pahaska|21048F09|USA:NE,Sioux Co.|1985
Hesperia pahaska pahaska|22057C05|USA:NM,Lincoln Co.|2020
0.002
c
mitochondrial
Hesperia pahaska hannawackeri|23049C06|USA:UT,Uintah Co.|1968
Hesperia pahaska hannawackeri|23049C02|USA:UT,Garfield Co.|1972
Hesperia pahaska hannawackeri|23049E06|USA:CO,Garfield Co.|1968
Hesperia pahaska hannawackeri|23049F06|USA:CO,Grand Co.|2000
Hesperia pahaska hannawackeri|23051A03|USA:AZ,Navajo Co.|1982
Hesperia pahaska hannawackeri|PAO566|PT|USA:CO,Mesa Co.|2017
Hesperia pahaska hannawackeri|22055G12|PT|USA:CO,Montrose Co.
Hesperia pahaska hannawackeri|22055G08|PT|USA:CO,Mesa Co.
Hesperia pahaska hannawackeri|22055G11|PT|USA:CO,Montrose Co.
Hesperia pahaska hannawackeri|23051C03|USA:UT,Emery Co.|1998
Hesperia pahaska hannawackeri|23049C03|USA:UT,Grand Co.|1975
Hesperia pahaska hannawackeri|23049C04|USA:UT,Grand Co.|1975
Hesperia pahaska hannawackeri|23049C08|USA:UT,Wayne Co.|1979
Hesperia pahaska hannawackeri|20045F05|PT|USA:UT,San Juan Co.
Hesperia pahaska hannawackeri|22055G10|PT|USA:CO,Delta Co.
Hesperia pahaska hannawackeri|22055G09|PT|USA:CO,Mesa Co.
Hesperia pahaska hannawackeri|23049C07|USA:UT,San Juan Co.
Hesperia pahaska hannawackeri|23051C09|USA:AZ,Coconino Co.
Hesperia pahaska hannawackeri|23049C05|USA:UT,Kane Co.|1979
Hesperia pahaska hannawackeri|23051B09|USA:UT,Kane Co.|1988
Hesperia pahaska hannawackeri|20045F06|HT|USA:UT,San Juan Co.
Hesperia pahaska hannawackeri|23051B10|USA:AZ,Coconino Co.
Hesperia pahaska hannawackeri|23049F04|USA:CO,San Miguel Co.
Hesperia pahaska hannawackeri|23049D03|USA:NV,Lincoln Co.|1984
Hesperia pahaska williamsi|22047D12|PT|USA:AZ,Mohave Co.|old
Hesperia pahaska williamsi|23049C11|USA:AZ,Cochise Co.|1980
Hesperia pahaska williamsi|23051C06|Mexico:Son|1986
Hesperia pahaska williamsi|23049G09|Mexico:Son|1984
Hesperia pahaska williamsi|23051C11|USA:AZ,Santa Cruz Co.|1988
Hesperia pahaska williamsi|23051C07|Mexico:Chih/Son|1985
Hesperia pahaska williamsi|8279|USA:AZ,Pinal Co.|2017
Hesperia pahaska williamsi|23049C12|USA:AZ,Santa Cruz Co.|1980
Hesperia pahaska williamsi|15096B10|HT|USA:AZ,Pima Co.|1923
Hesperia pahaska williamsi|20067B03|Mexico:Son|1998
Hesperia pahaska williamsi|23051B12|USA:AZ,Santa Cruz Co.|1995
Hesperia pahaska williamsi|20067B04|Mexico:Son|2003
Hesperia pahaska williamsi|20067B02|Mexico:Son|2004
Hesperia pahaska williamsi|23049C09|USA:UT,Washington Co.|1955
Hesperia pahaska williamsi|23051C01|USA:AZ,Gila Co.|1988
Hesperia pahaska williamsi|23051B05|USA:AZ,Graham Co.|1963
Hesperia pahaska williamsi|23049G06|USA:AZ,Yavapai Co.|1965
Hesperia pahaska williamsi|23049D02|USA:AZ,Mohave Co.|1979
Hesperia pahaska williamsi|23049H11|USA:AZ,Yavapai Co.|1980
Hesperia pahaska martini|23051A04|PT|USA:CA,San Bernardino Co.
Hesperia pahaska martini|23049D10|PT|USA:CA,San Bernardino Co.
Hesperia pahaska martini|20067B05|USA:CA,San Bernardino Co.|1959
Hesperia pahaska martini|21048F11|USA:CA,San Bernardino Co.|1978
Hesperia pahaska martini|21048F12|USA:CA,San Bernardino Co.|1981
Hesperia pahaska martini|21048G01|USA:CA,San Bernardino Co.|1978
Hesperia pahaska martini|15105D04|HT|USA:CA,San Bernardino Co.
Hesperia pahaska martini|23051C05|USA:NV,Clark Co.|1969
Hesperia pahaska martini|23049F11|USA:NV,Clark Co.|1969
Hesperia pahaska martini|23051B11|USA:NV,White Pine Co.|1969
Hesperia pahaska tehaska ssp. n.|23051B01|PT|USA:TX,Brewster Co.
Hesperia pahaska tehaska ssp. n.|23049B04|PT|USA:TX,Presidio Co.
Hesperia pahaska tehaska ssp. n.|23049B07|PT|USA:TX,Pecos Co.|1973
Hesperia pahaska tehaska ssp. n.|23049B05|PT|USA:TX,Presidio Co.
Hesperia pahaska tehaska ssp. n.|23051B02|PT|USA:TX,Brewster Co.
Hesperia pahaska tehaska ssp. n.|23049B09|HT|USA:TX,Jeff Davis Co.
Hesperia pahaska tehaska ssp. n.|23051A01|PT|USA:TX,Brewster Co.
Hesperia pahaska tehaska ssp. n.|11128|PT|USA:TX,Jeff Davis Co.|2018
Hesperia pahaska tehaska ssp. n.|10967|PT|USA:TX,Jeff Davis Co.|2018
Hesperia pahaska tehaska ssp. n.|23051B03|PT|USA:TX,Culberson Co.
Hesperia pahaska tehaska ssp. n.|23049B08|PT|USA:TX,Pecos Co.|1974
Hesperia pahaska tehaska ssp. n.|23049B10|PT|USA:TX,Jeff Davis Co.
Hesperia pahaska tehaska ssp. n.|23051C10|PT|USA:TX,McCulloch Co.
Hesperia pahaska hidalgo ssp. n.|23049G08|HT|Mexico:Hgo|1981
Hesperia pahaska hidalgo ssp. n.|24097G03|PT|Mexico:Hgo|1981
Hesperia pahaska bajanorta ssp. n.|23049G10|HT|Mexico:BC Norte
Hesperia pahaska bajanorta ssp. n.|23049H01|PT|Mexico:BC Norte
Hesperia pahaska bajanorta ssp. n.|23049G12|PT|Mexico:BC Norte
Hesperia pahaska bajanorta ssp. n.|23049G11|PT|Mexico:BC
Hesperia pahaska pahaska|22057C05|USA:NM,Lincoln Co.|2020
Hesperia pahaska pahaska|21048F09|USA:NE,Sioux Co.|1985
0.003

Fig. 126 (see previous page). Phylogenetic trees of *Hesperia pahaska* specimens constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,407,714 positions, **b)** the Z chromosome, based on 341,715 positions, and **c)** the mitochondrial genome. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different subspecies are colored differently: *H. pahaska hannawackeri* (blue), *H. pahaska williamsi* (olive), *H. pahaska martini* (cyan), *H. pahaska tehaska* **sp. n.** (purple), *H. pahaska hidalgo* **sp. n.** (red), *H. pahaska bajanorta* **sp. n.** (green), and *H. pahaska pahaska* (black, only two specimens shown). Holotypes are labeled in magenta. Gaps in branches indicate that a segment of a branch was cut out to reduce its length (to allow an increase in the font size), i.e., a branch with a gap is longer than shown.

Fig. 127. *Hesperia pahaska tehaska* **sp. n.** holotype ♂ NVG-23049B09 in dorsal (left) and ventral (right) views, data in text. All *Hesperia* holotypes (Figs. 127, 129, 130) are shown at the same scale to facilitate comparisons.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 127, bears the following six printed (text in italics handwritten) rectangular labels, five white: [TEXAS: | JEFF DAVIS COUNTY | Davis Mtns. | Fisher Hill 6141'], [William W. & | Nadine M. McGuire | coll. *28-VIII-77*], [Collection of | William W. McGuire], [FSCA | Florida State Collection | of Arthropods], [DNA sample ID: | NVG-23049B09 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Hesperia pahaska | tehaska Grishin]. **Paratypes:** 7♂♂ and 5♀♀ in MGCL unless stated otherwise: USA, Texas: 1♂ NVG-23051B03 Culberson Co., 12 mi S and 10 mi E of Van Horn, 11-May-1973, J. Harry leg.; Jeff Davis Co., Davis Mnts.: 1♂ NVG-10967 SH118 S of McDonald Observatory, GPS 30.6597, −104.0232, 9-Apr-2018, N. V. Grishin leg. [UTSW], 1♀ NVG-23049B10, 29 mi W of Fort Davis, 28-Aug-1977, W. W. & N. M. McGuire leg., and 1♀ NVG-11128 SH118 nr. Caldwell Ranch, GPS 30.736725, −104.139271, 18-May-2018, N. V. Grishin & J. Zhang leg. [UTSW]; Presidio Co.: 1♂ NVG-23049B04 3 mi N of Shafter, 29-May-1973, W. W. & N. M. McGuire and 1♀ NVG-23049B05 Shafter, 9-Jun-1961, H. A. Freeman leg.; Brewster Co.: 1♂ NVG-23051A01 10 mi N of Persimmon Gap, 26-May-2008, C. Bordelon & E. Knudson leg., 1♂ NVG-23051B01 USH90, ca 35 mi W of Sanderson, 8-Jun-1974, W. W. McGuire leg., and 1♀ NVG-23051B02 USH90, 14 mi E of Marathon, coll. 26-Jul-1977, ex ovum, W. W. & N. M. McGuire leg.; Pecos Co., USH90, 20 mi W of Sanderson, W. W. McGuire leg.: 1♂ NVG-23049B07 20-May-1973 and 1♀ NVG-23049B08 9-Jun-1974; and 1♂ NVG-23051C10 McCulloch Co., Heart of Texas Roadside, 24-Apr-1980, D. Bauer leg.

Type locality. USA: Texas, Jeff Davis Co., Davis Mts., Fisher Hill, elevation 6141', approx. GPS 30.6972, −104.0967.

Etymology. The name is formed from the type locality and is treated as a feminine noun in apposition.

Distribution. Central to West Texas (USA).

Hesperia pahaska hidalgo Grishin, new subspecies

http://zoobank.org/1ADE0404-E9CA-4E0B-9003-A0A325B6CDBD

(Figs. 126 part, 128 part, 129)

Definition and diagnosis. Genomic analysis of two specimens of *Hesperia pahaska* Leussler, 1938 (type locality in USA: Nebraska, Sioux Co.) from Hidalgo, Mexico, places them separately from other

populations in a clade genetically differentiated at least at the subspecies level (Fig. 126); e.g., their COI barcodes differ from geographically closest *Hesperia pahaska tehaska* **ssp. n.** by 1.7% (11 bp), and, therefore, represent a new subspecies. This new subspecies keys to "*Hesperia columbia pahaska*" (M.10.5.(b)) in Evans (1955) and differs from other subspecies of *H. pahaska* by being smaller, darker, especially on the ventral hindwing, with larger submarginal pale spots near the forewing apex and redder, not greenish or yellowish, tones of the ventral side of wings, and by submarginal spots in forewing cells M_1-M_2 and M_2-M_3 being longer and reaching closer to the wing outer margin. Due to the cryptic nature of this subspecies and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly838.4.2:G156T, aly838.4.2:G159A, aly839.15.3:G75A, aly839.15.3:A76C, aly613.3.6:A141G; and COI barcode: T250C, C282T, G389A, T485C, A625G.

Barcode sequence of the holotype. Sample NVG-23049G08, GenBank PV550056, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCTGGTATATTAGGAACTTCATTAAGTTTAT
TAATTCGAACAGAATTAGGTAATCCTGGATCTTTAATTGGAGATGACCAAATTTATAAT
ACTATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATGCCAATTATAAT
TGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTC
CACGTATAAATAACATAAGATTTTGAATATTACCACCTTCATTAATATTATTAATTTCA
AGAAGAATTGTAGAAAATGGTGCTGGAACAGGCTGAACTGTTTATCCTCCTTTATCCTC
TAATATTGCTCATCAAGGATCTTCTGTTGATTTAACAATTTTTTCTCTTCACTTAGCTG
GAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAATT
AAAAACTTATCTCTTGATCAAATACCTTTATTTGTTTGATCTGTAGGAATTACAGCATT
ATTATTACTTTTATCTTTACCTGTATTAGCAGGAGCTATTACTATACTACTTACTGACC
GAAATTTAAATACTTCTTTTTTCGATCCAGCAGGGGGAGGAGATCCAATTTTATATCAACATTTATTT

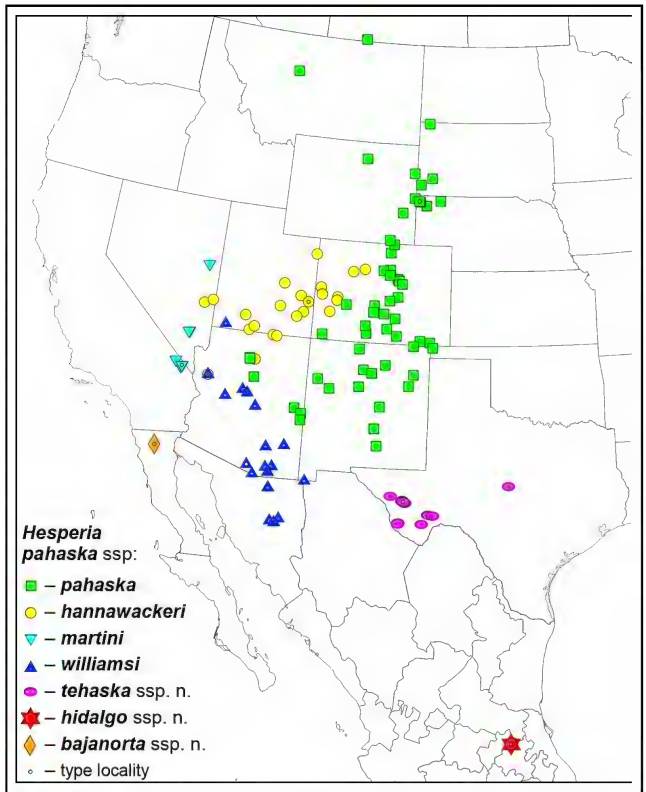


Fig. 128. A map of sequenced specimens of *Hesperia pahaska* subspecies: *pahaska* (green squares), *hannawackeri* (yellow circles), *martini* (cyan inverted triangles), *williamsi* (blue triangles), *tehaska* **ssp. n.** (magenta ovals), *hidalgo* **ssp. n.** (red star), *bajanorta* **ssp. n.** (orange diamond). The type localities of subspecies are marked with tiny white circles inside symbols. Four U.S. subspecies converge near the NV–UT–AZ tripoint, where mixed populations occur, and subspecies assignment is currently tentative—if possible at all.

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 129, bears the following six rectangular labels (1st handwritten, others printed), five white: [MEXICO. Hidalgo: | Rt.85, 90.4 mi | N. Pachuca, 4-Aug-1981 | leg. Douglas Mullins], [Hesperia | pahaska williamsi | Lindsey | Det. W.W. McGuire], [Collection of | William W. McGuire], [FSCA | Florida State Collection | of Arthropods], [DNA sample ID: | NVG-23049G08 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Hesperia pahaska | hidalgo Grishin]. **Paratype:** 1♂ NVG-24097G03 with the same data as the holotype.

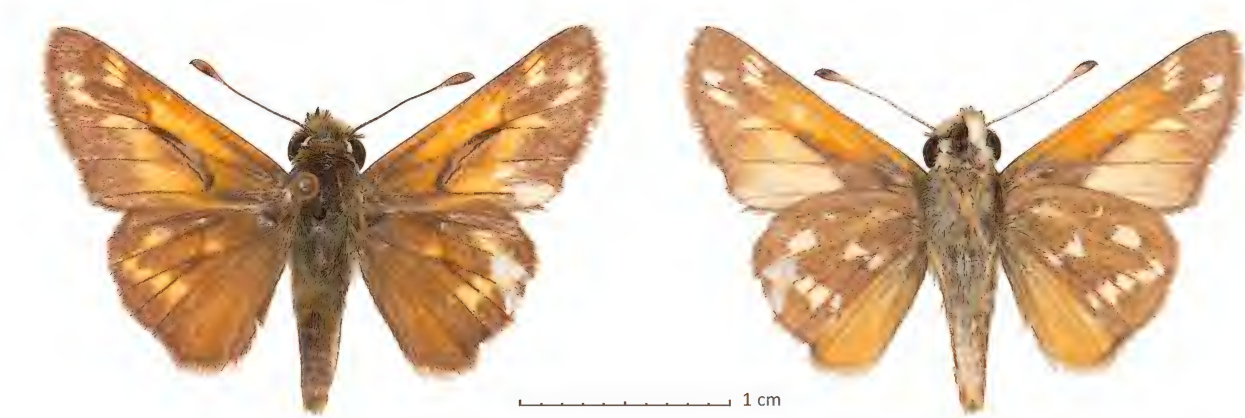


Fig. 129. *Hesperia pahaska hidalgo* **sp. n.** holotype ♂ NVG-23049G08 in dorsal (left) and ventral (right) views, data in text.

Type locality. Mexico: Hidalgo, Rt. 85, 90.4 mi north of Pachuca.

Etymology. The name of the state with the type locality is used as the name of the new subspecies and is treated as a noun in apposition.

Distribution. Currently known only from the state of Hidalgo in Mexico.

Hesperia pahaska bajanorta Grishin, new subspecies

http://zoobank.org/4F174661-E48E-4C06-AB91-B2451395772F

(Figs. 126 part, 128 part, 130)

Definition and diagnosis. Genomic analysis of two specimens of *Hesperia pahaska* Leussler, 1938 (type locality in USA: Nebraska, Sioux Co.) from Baja California, Mexico, places them away from other populations in a clade genetically differentiated at least at the subspecies level (Fig. 126); e.g., their COI barcodes differ from those of their possible sister *H. pahaska hidalgo* **ssp. n.** by 1.8% (12 bp), and, therefore, represent a new subspecies. This new subspecies keys to "*Hesperia columbia pahaska*" (M.10.5.(b)) in Evans (1955) and differs from other subspecies of *H. pahaska* by a combination of the following characters: paler and more uniformly colored, with paler, more diffuse, and in some specimens narrower marginal brown areas on wings above, especially on the hindwing, which is mostly orange; orange-yellow subapical and submarginal spots on the forewing weakly stand out and are smaller; and smaller white spots and yellower (not greener or redder) hue of the ventral side of wings. In DNA, a combination of the following base pairs is diagnostic in the nuclear genome: aly18826.15.6:T99C, aly18826.15.6:T105A, aly18826.15.6:G135A, aly128.1.3:G183A, aly128.1.3:T204C; and COI barcode: C106T, G166A, A242T, T334C, T346C.

Barcode sequence of the holotype. Sample NVG-23049G10, GenBank PV550057, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCTGGTATATTAGGAACTTCATTAAGTTTATTAATTCGAACAGAATTAGGTAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCTGACATAGCTTTTCCACGTT
TAAATAATATAAGATTTTGAATATTACCACCTTCATTAACATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGAACAGGCTGAACCGTTTATCCTCCCTTATCCTCTAATATTGC
TCATCAAGGATCTTCTGTTGATTTAGCAATTTTTTCTCTTCACTTAGCTGGAATTTCATCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAATTAAAAACTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGAATTACAGCATTATTATTACTTTTATCTTTACCTGTATTAGCAGGAGCTATTACTATATTACTTACTGACCGAAATTTAAATACTT
CTTTTTTTGATCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 130, bears the following six rectangular labels (2nd handwritten, others printed with handwritten text shown in italics), five white: [MEXICO. | Baja California Norte: | 6 mi. NW Laguna Hanson, | Sierra Juarez, *22*-Jun-1980 | leg WW McGuire], [+], [Collection of | William W. McGuire], [FSCA | Florida State Collection | of Arthropods], [DNA sample ID: | NVG-23049G10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Hesperia pahaska | bajanorta Grishin]. **Paratypes:** 8♂♂ the same data as the holotype, except as indicated: 7♂♂ NVG-23049G11, NVG-23049H01, and five not sampled for DNA; and 1♂ NVG-23049G12 4 Jun-1980.

Fig. 130. *Hesperia pahaska bajanorta* **sp. n.** holotype ♂ NVG-23049G10 in dorsal (left) and ventral (right) views, data in text.

Type locality. Mexico: Baja California Norte, 6 mi northwest of Laguna Hanson, Sierra Juarez.

Etymology. The name is formed from the name of the Mexican state with the type locality and is treated as a feminine noun in apposition.

Distribution. Mexico: Baja California Norte.

The genus *Ochlodes* Scudder, 1872 consists of four subgenera

Inspection of the genomic phylogeny of Hesperiina reveals that the genus *Ochlodes* Scudder, 1872 (type species *Hesperia nemorum* Boisduval, 1852, currently regarded as a subspecies of *Hesperia agricola* Boisduval, 1852) experienced deep radiation (Fig. 131) and consists of four major clades. We define these clades as subgenera, three of which do not have available names and, therefore, are new, described below.

Ochloba Grishin, new subgenus

http://zoobank.org/C5B39850-C8BB-42CB-AD5A-514584AEE3DB

Type species. *Poanes batesi* Bell, 1935.

Definition. In the genomic phylogeny of *Ochlodes* Scudder, 1872, the first prominent clade, which is sister to the rest, currently includes a single species, the only member of the genus from the Caribbean Islands, and represents a new subgenus (Fig. 131). This new subgenus differs from its relatives by a combination of the following characters: the two parts of the stigma are aligned perfectly with each other (the end of one is not offset compared to the beginning of the other), ventral hindwing and the apex of ventral forewing are green-colored, valva with a larger cleft between harpe and ampulla, the aedeagus is broad, without a long style but with a long pack of cornuti. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly536.34.1:T45A, aly216.67.2:A123G, aly72.25.3:G69A, aly1113.24.1:G617A, aly727.16.4:T106C; and in COI barcode: T46A, A76G, A280G, T379C, T424A.

Etymology. The name is a fusion of the names of the genus and the type species of the subgenus (first syllable): *Ochlo*[des] + *ba*[tesi]. The name is a feminine noun in the nominative singular.

Species included. Only the type species (i.e., *Poanes batesi* Bell, 1935).

Parent taxon. Genus *Ochlodes* Scudder, 1872.

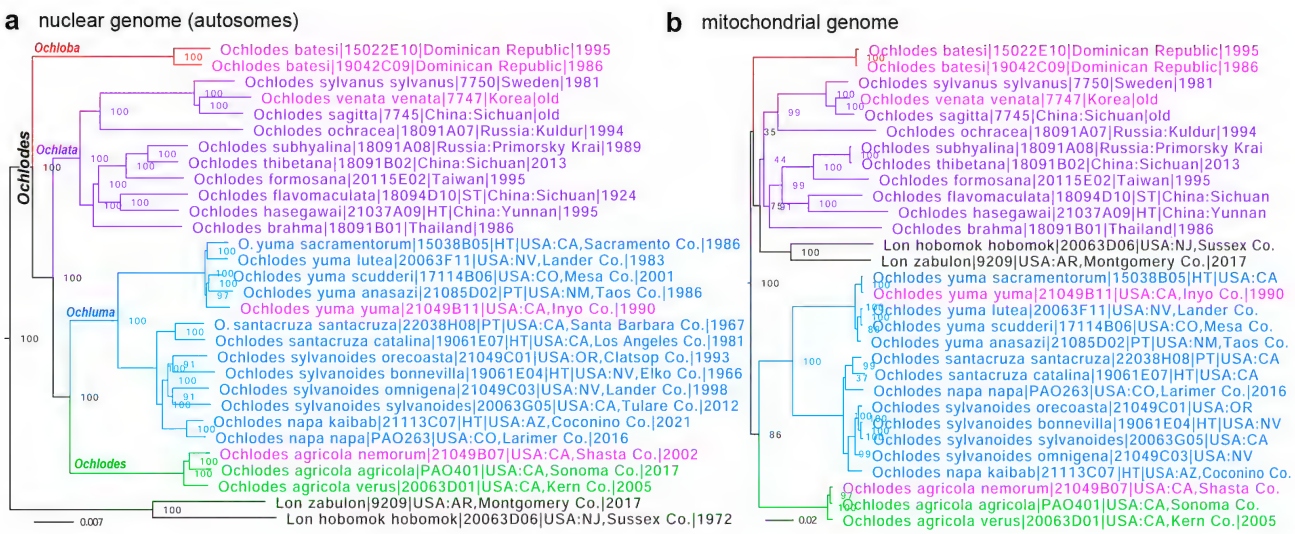


Fig. 131. Phylogenetic trees of *Ochlodes* inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 13,712,217 positions, and **b)** the mitochondrial genome. Different subgenera are shown in different colors: *Ochloba* **subgen. n.** (red). *Ochlata* **subgen. n.** (purple), *Ochluma* **subgen. n.** (blue), and *Ochlodes* (green) and labeled above corresponding branches in the nuclear genome tree. Type species of subgenera are labeled in magenta.

Ochlata Grishin, new subgenus

http://zoobank.org/6E20DE25-20C7-4367-8A95-0FE0044C2C88

Type species. *Hesperia venata* Bremer & Grey, 1853.

Definition. In the genomic phylogeny of *Ochlodes* Scudder, 1872, the last prominent clade consists of all Old World species and represents a new subgenus (Fig. 131). This new subgenus differs from its relatives by a combination of the following characters: the two parts of the stigma are at least slightly offset from each other; ventral hindwing and the apex of ventral forewing are yellow to brown, sometimes with olive overscaling but not bright-green; valva may have a prominent cleft between harpe and ampulla in some species, while in others harpe touches the ampulla, the aedeagus is narrower, with a long style and several cornuti. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly2682.1.6:G81A, aly2178.36.1:C129T, aly2250.11.1:A174G, aly256.7.8:T177A, aly159.16.1:G96A; and in COI barcode: A85T, 232T or C (not A), T325A, T514T, T520T.

Etymology. The name is a fusion of the names of the genus and the type species of the subgenus: *Ochl*[odes] + [ven]*ata*. The name is a feminine noun in the nominative singular.

Species included. All Old World species of *Ochlodes* Scudder, 1872: the type species (i.e., *Hesperia venata* Bremer & Grey, 1853), *Pamphila bouddha* Mabille, 1876, *Pamphila brahma* Moore, 1878, *Augiades crataeis* Leech, 1893, *Ochlodes flavomaculata* Evans, 1949, *Augiades formosana* Bremer & Grey, 1853, *Ochlodes hasegawai* Chiba & Tsukiyama, 1996, *Ochlodes klapperichii* Evans, 1940, *Ochlodes lanta* Evans, 1939, *Ochlodes linga* Evans, 1939, *Pamphila ochracea* Bremer, 1861, *Ochlodes sagitta* Hemming, 1934, *Augiades similis* Leech, 1893, *Pamphila siva* Moore, 1878, *Hesperia subhyalina* Bremer & Grey, 1853, *Papilio sylvanus* Esper, 1777, *Pamphila thibetana* Oberthür, 1886, including taxa currently treated as their subspecies and synonyms.

Parent taxon. Genus *Ochlodes* Scudder, 1872.

Ochluma Grishin, new subgenus

http://zoobank.org/014C323C-B441-41A0-A97F-EA3D552549D7/

Type species. *Hesperia yuma* W. H. Edwards, 1873.

Definition. In the genomic phylogeny of *Ochlodes* Scudder, 1872, the second prominent clade consists of several North American species and represents a new subgenus (Fig. 131). This new subgenus differs from its relatives by a combination of the following characters: the two parts of the stigma are at least slightly offset from each other; ventral hindwing and the apex of ventral forewing are yellow to brown, sometimes with olive overscaling but not bright-green; valva is broader and lacks a prominent cleft between the harpe and ampulla, the aedeagus is medium in width or narrow, with a shorter and more robust style, terminal spike, and several larger cornuti, uncus and gnathos arms are approximately the same in length, extended and thinner than in most relatives, the juxta is broad and rounded, leaf-like, as wide as the distance between the ends of the process and the spike of the aedeagus. In DNA, a combination of the following characters is diagnostic in the nuclear genome: aly214.15.5:C75T, aly1249.14.7:G840A, aly119.1.1:A444G, aly1916.7.3:G132A, aly2874.9.7:G78A; and in COI barcode: T10C or T142C, T232A, T292T, A415T, T478C, T499C or/and T553C.

Etymology. The name is a fusion of the names of the genus and the type species of the subgenus: *Ochl*[odes] + [y]*uma*. The name is a feminine noun in the nominative singular.

Species included. The type species (i.e., *Hesperia yuma* W. H. Edwards, 1873), *Hesperia sylvanoides* Boisduval, 1852, *Hesperia napa* W. H. Edwards, 1865, and *Ochlodes sylvanoides santacruza* J. Scott, 1981, including their subspecies and synonyms.

Parent taxon. Genus *Ochlodes* Scudder, 1872.

Lon co Grishin, 2023 and *Lon ma* Grishin, 2023 are sympatric in Monteverde, Costa Rica

Genomic analysis reveals that *Lon co* Grishin, 2023 (type locality in Mexico: Guerrero) and *Lon ma* Grishin, 2023 (type locality in Panama) are sympatric in Monteverde, Puntarenas Province in Costa Rica (Fig. 132). They have been collected by different collectors in different years, which minimizes the chance of mislabeling. Moreover, one specimen of each species was collected there (elevation 1280 m) on September 7–9, 1988 by P. F. Milner (NVG-24065F01, Fig. 133b, h and NVG-24065E12, Fig. 133f, l), and also in March 1987, J. Brenner collection (NVG-24065E10, Fig. 133a, g and NVG-23048E11, Fig. 133d, j), as indicated on identical labels (within each pair) of these specimens. We use this opportunity to refine phenotypic characters for the identification of these species in the area of sympatry. Three males of each species from the Puntarenas Province are shown in (Fig. 133). We noticed five characters that may be useful for identification, pointed at by green arrows in the first specimen (Fig. 133a, g): (1) in *L. co*, the dorsal hindwing discal orange patch extends deeper into cell CuA_2-1A+2A and there is somewhat diffuse orange overscaling along and around the vein 1A+2A forming a "ray", which is absent in *L. ma*; (2) the dorsal hindwing brown margin is wider in *L. co* and narrower, especially between veins M_1 and M_3, in *L. ma*; (3) the ventral hindwing marginal area in *L. co* is darker than in *L. ma* towards the tornus, e.g., between veins M_1 and M_3; (4) the discal brown spot in the cell CuA_2-1A+2A of the ventral hindwing is relatively smaller in *L. co* than in *L. ma*, and brown spots in this row directed towards the apex are more similar in size in *L. co* than in *L. ma*, in which the inner spot is noticeably larger than others; (5) the anal cell of the ventral hindwing is yellower in *L. co* than in *L. ma*, in which it is overscaled with brown.

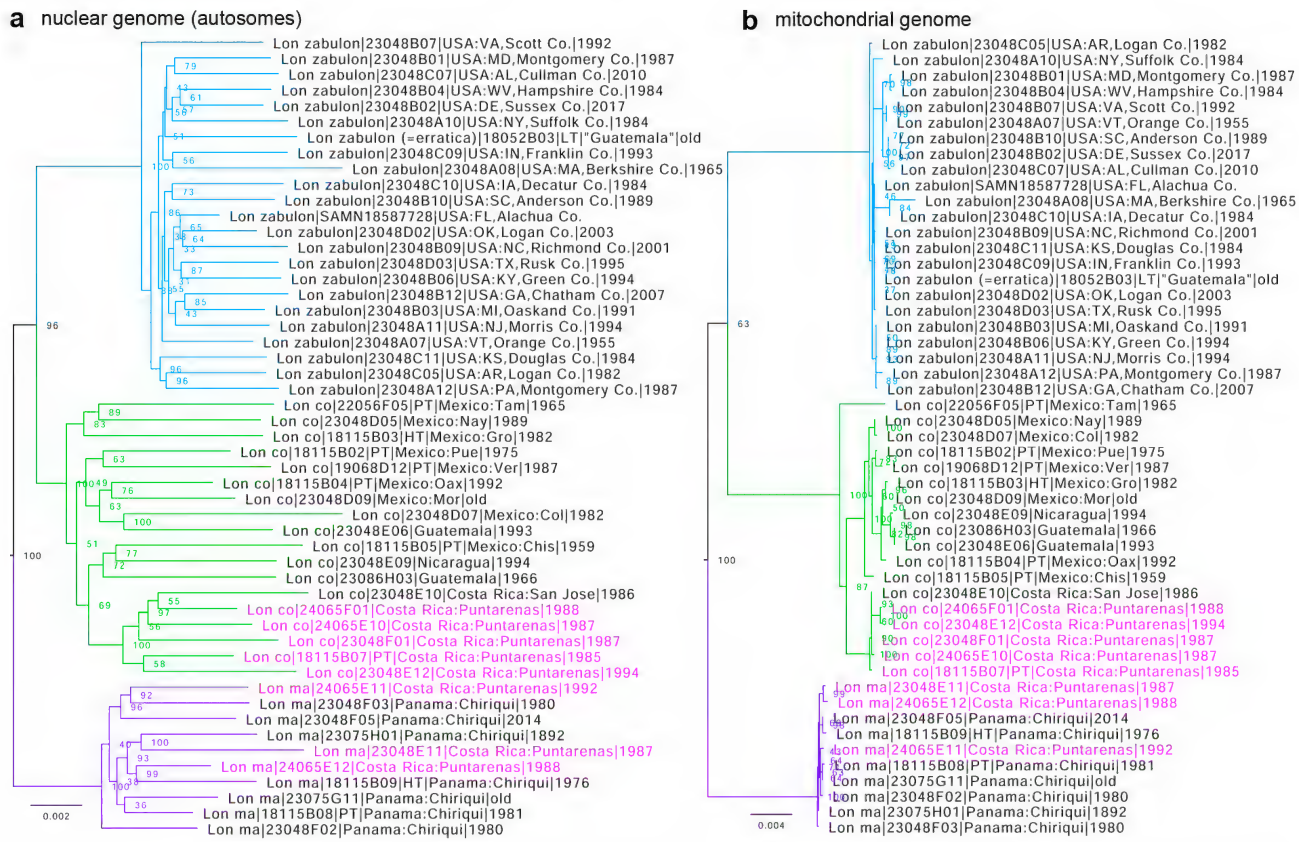


Fig. 132. Phylogenetic trees of three species of *Lon* inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 807,423 positions, and **b)** the mitochondrial genome. Specimens from Puntarenas Province, Costa Rica, are labeled in magenta. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Different species are in different colors: *L. zabulon* (blue), *L. co* (green), and *L. ma* (purple). The sequence of SAMN18587728 is taken from the alignment provided in Kawahara et al. (2023).

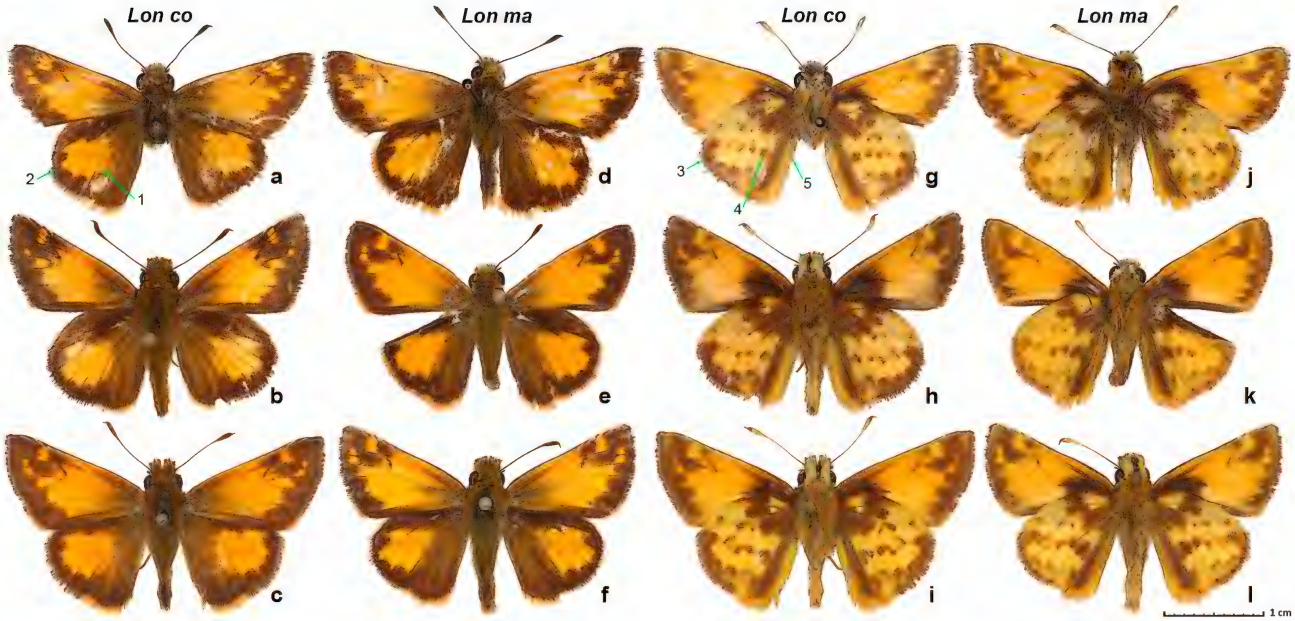


Fig. 133. *Lon* males from Costa Rica: Puntarenas Prov., in dorsal (left half, **a–f**) and ventral (right half, **g–l**) views: *L. co* in the 1st and 3rd column (**a–c**, **g–i**) and *L. ma* in the 2nd and 4th column (**d–f**, **j–l**), the same specimen is shown in the same position in the left and right halves of the image. Green arrows point to characters useful for identification of these species, numbered 1 to 5, see text. Specimens were collected in Monteverde and are in MGCL, except as indicated. **a**, **g**) NVG-24065E10, Mar-1987, J. Brenner coll.; **b**, **h**) NVG-24065F01, 1280 m, 7-9-Sep-1988, P. F. Milner leg.; **c**, **i**) NVG-18115B07, USNMENT 01531555 PT, 1300 m, 18-May-1985, J. A. Chemsak leg. [USNM]; **d**, **j**) NVG-23048E11, Mar-1987, J. Brenner coll.; **e**, **k**) NVG-24065E11 Las Alturas, 1400 m, 5-Jul-1992 A. Sourakov leg.; **f**, **l**) NVG-24065E12, 1280 m, 7-9-Sep-1988, P. F. Milner leg.

Vacerra tama Grishin, new species

http://zoobank.org/4774ED12-2163-4DB9-B8ED-DE65D9247593

(Figs. 134 part, 135–136)

Definition and diagnosis. The nuclear genomic tree of *Vacerra* Godman, 1900 (type species *Hesperia litana* Hewitson, 1866) reveals that a specimen from Mexico: Tamaulipas (NVG-22056G03) is a distant sister of *Vacerra gayra* (Dyar, 1918) (type locality in Mexico: Guerrero) and is strongly differentiated from it genetically (Fig. 134); e.g., their COI barcodes differ by 4.7% (31 bp). Therefore, this specimen represents a new species. This new species is phenotypically similar to *V. gayra* and keys to "*Vacerra egla gayra*" (O.8.2.(a)) in Evans (1955) but differs from it by a more aligned basal margin of a paler marginal band on the ventral hindwing in cells Sc+R_1-RS and RS-M_1, so that the brown ground color basad of the band does not protrude more strongly in the cell RS-M_1 than in the cell Sc+R_1-RS. In *V. gayra*, the basal margin is stepwise in cells RS-M_1 and Sc+R_1-RS, so that the brown ground color reaches closer to the wing outer margin in cell RS-M_1 than in cell Sc+R_1-RS. Due to unexplored individual variation and possibly cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly412.8.5:A210G, aly9588.18.2:G48A, aly2275.10.11:C135T, aly2275.10.11:A159C, aly16031.3.3:T46C, aly16031.3.3:G48G (not A), aly318.28.9:T294T (not C), aly318.28.9:G300G (not C), aly925.11.9:C336C (not T), aly925.11.9: T342T (not C); and COI barcode: T46A, A49C, T64C, A199G, T439C, T514C.

Barcode sequence of the holotype. Sample NVG-22056G03, GenBank PV550059, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATACTAGGAACATCCCTAAGACTATTAATCCGTACAGAATTAGGTAATCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCAATTATAATTGGAGGATTTGGAAATTGATTGGTTCCTCTTATATTAGGAGCTCCAGATATAGCTTTTCCACGAA
TAAATAATATAAGATTTTGAATATTACCCCCCTCATTAACTTTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACTGGTTGAACTGTATATCCACCTTTATCTTCAAATATTGC
CCATCAAGGAGCTTCAGTTGATTTAGCAATTTTTTCTCTTCATTTAGCAGGTATTTCTTCTATTCTAGGAGCTATCAACTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATAAAATACCTTTATTTGTTTGATCCGTGGGTATTACAGCCTTATTATTACTTTTATCTTTACCTGTTTTAGCTGGAGCTATTACTATATTACTTACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the collection of the Biodiversity Center, University of Texas at Austin, Austin, TX, USA (TMMC), illustrated in Fig. 135 (genitalia Fig. 136), bears the following five

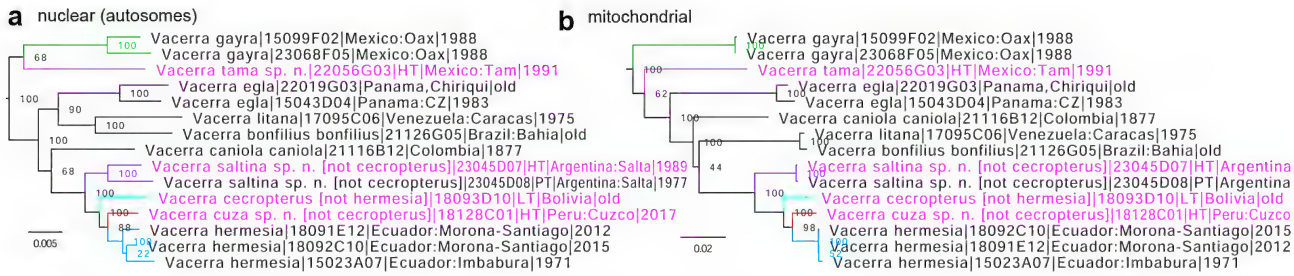


Fig. 134. Phylogenetic trees of *Vacerra* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome. Primary type specimens are labeled in magenta, and branches of selected species are colored differently: *V. gayra* (green), *V. tama* **sp. n.** (magenta), *V. saltina* **sp. n.** (purple), *V. cecropterus* **stat. rest.** (cyan), *V. cuza* **sp. n.** (red), and *V. hermesia* (blue).

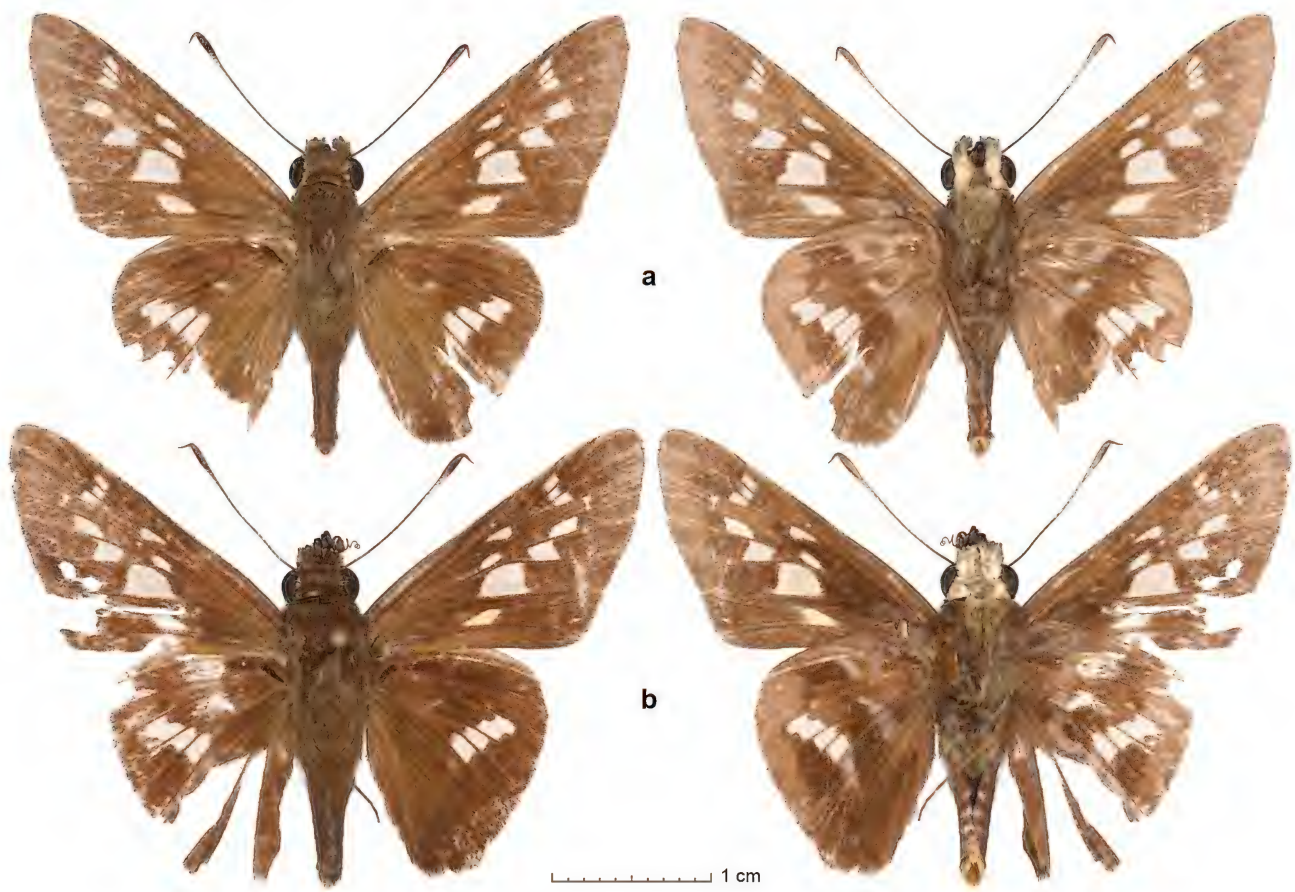


Fig. 135. *Vacerra tama* **sp. n.** males in dorsal (left) and ventral (right) views, data in text: **a)** holotype NVG-22056G03 and **b)** paratype NVG-24015D04.

printed rectangular labels, four white: [TA.GomezFarias.017 | 1–3kSSW ElAzteca | DurdenCJ 91145A36], [DNA sample ID: | NVG-22056G03 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24015E06 | c/o Nick V. Grishin], [genitalia: | NVG241114-12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Vacerra tama | Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. The holotype was collected on 25-May-1991 (i.e., "91145": day 145 of 1991, A36 is the collection event referring to this specimen in Durden's master catalog), and 017 after "GomezFarias" on the first label is the code for the locality "1 to 3k SSW El Azteca towards Gomez Farias." **Paratype:** 1♂ NVG-24015D04, the same data as the holotype, but 1–4 km N of Gomez Farias, 350 m, 19-Aug-1972.

Type locality. Mexico: Tamaulipas, Gomez Farias, 1–3 km south-southwest of El Azteca towards Gomez Farias.

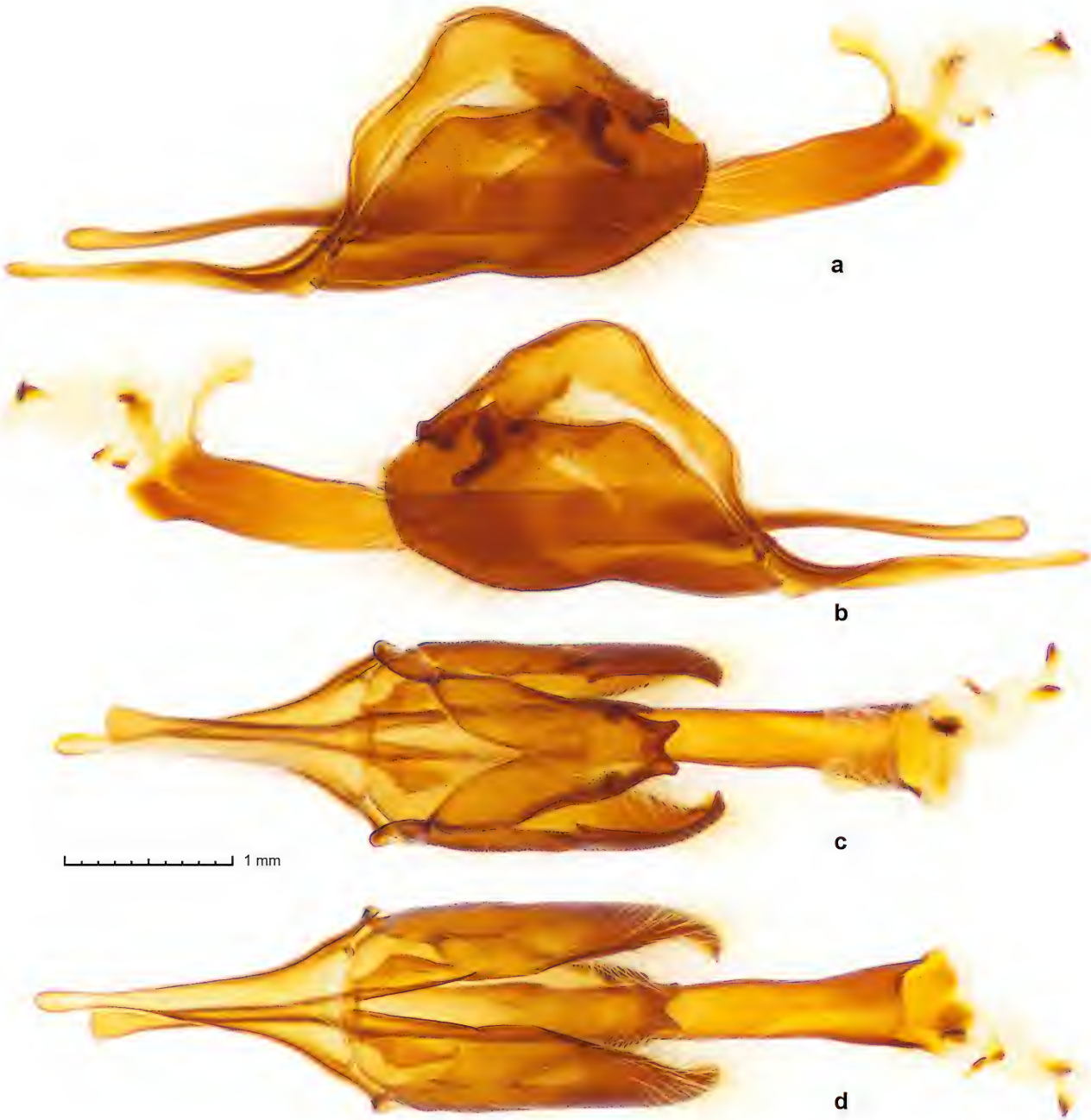


Fig. 136. Male genitalia of *Vacerra tama* **sp. n.** holotype NVG-22056G03 in different views: **a)** left lateral, **b)** right lateral, **c)** dorsal, and **d)** ventral.

Etymology. The first two syllables of the Mexican state name with the type locality of this species are used as the name. The name is treated as a noun in apposition.

Distribution. Currently known only from northeastern Mexico.

Vacerra cecropterus (Draudt, 1923) is a species distinct from *Vacerra hermesia* (Hewitson, 1870)

Genomic analysis of the lectotype of *Xeniades cecropterus* Draudt, 1923 (type locality in Bolivia: Rio Zongo, sequenced as NVG-18093D10) that is currently treated as a subspecies of *Vacerra hermesia*

(Hewitson, 1870) (type locality in Ecuador) is genetically differentiated from it at the species level (Fig. 134); e.g., their COI barcodes differ by 2.6% (17 bp). The two taxa also differ phenotypically as detailed by Evans (1955). Therefore, we propose that *Vacerra cecropterus* (Draudt, 1923), **stat. rest.** is a species distinct from *Vacerra hermesia* (Hewitson, 1870).

Vacerra saltina Grishin, new species

http://zoobank.org/22E207BC-AB16-4EA6-9445-4B055AB7D0DC

(Figs. 134 part, 137–138)

Definition and diagnosis. Genomic sequencing of a pair of specimens from Salta, Argentina, identified as "*Vacerra hermesia cecropterus*" reveals that they are not monophyletic with the lectotype of *Vacerra cecropterus* (Draudt, 1923), **stat. rest.** (type locality in Bolivia: Rio Zongo, sequenced as NVG-18093D10) and are instead sister to both *V. cecropterus* and *Vacerra hermesia* (Hewitson, 1870) (type locality in Ecuador), being genetically differentiated from them at the species level (Fig. 134); e.g., their COI barcodes differ by 2.7% (18 bp) (from *V. cecropterus*) and 3.2% (21 bp) (from *V. hermesia*). Therefore, these Argentinian specimens represent a new species. This new species keys to "*Vacerra hermesia cecropterus*" (O.8.7.(b)) in Evans (1955) but differs from its relatives by a combination of the following characters: subdued green dorsal overscaling that does not strongly stand out and is more olive-brown (not prominently blue-green as in *V. hermesia*); the hyaline spot in the cell CuA_1-CuA_2 being larger and more rectangular with less rounded corners and more aligned with the discal cell spot along their proximal margins: the two spots nearly form a short band separated by the vein; while in other species the spot in the cell CuA_1-CuA_2 is rounder, especially at the anterior proximal angle, and is offset distad from the discal cell spot and is separated from it by a wider brown ground color area; a small but prominent cream-colored spot in the discal cell of the ventral hindwing; the lack of postdiscal cream-colored spots in ventral hindwing cells CuA_1-CuA_2 and CuA_2-1A+2A; and a size comparable to *V. cecropterus* and smaller than *V. hermesia*. Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly2627.10.2:G105A, aly159.12.16:C42G, aly159.12.16:G54C, aly2790.11.3:G762A, aly2790.11.3:G768A; and COI barcode: T205C, T212C, T278C, T508C, A631G.

Barcode sequence of the holotype. Sample NVG-23045D07, GenBank PV550060, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATACTAGGAACTTCACTAAGACTATTAATTCGTACAGAATTAGGTAACCCAGGATCTTTAATTGGAGACGATCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTCTTTATAGTTATACCAATTATAATCGGAGGATTTGGAAATTGATTAGTTCCCCTTATACTAGGGGCCCCAGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATATTACCCCCATCACTAACATTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACCGGTTGAACTGTTTATCCACCTCTATCTTCAAATATTGC
CCATCAAGGAGCTTCTGTTGATTTAGCAATTTTTTCTCTTCATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTTGTCTGATCTGTAGGTATTACAGCTTTATTATTACTTTTATCTTTACCTGTTTTAGCTGGAGCTATTACCATATTACTTACTGATCGAAATTTAAATACTT
CATTTTTTGACCCAGCAGGAGGAGGGGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 137 (genitalia Fig. 138), bears the following seven printed rectangular labels, six white: [ARGENTINA Salta | (Oran) Agua Blanca | to Angosto, Rt

Fig. 137. *Vacerra saltina* **sp. n.** holotype ♂ NVG-23045D07 in dorsal (left) and ventral (right) views, data in text.

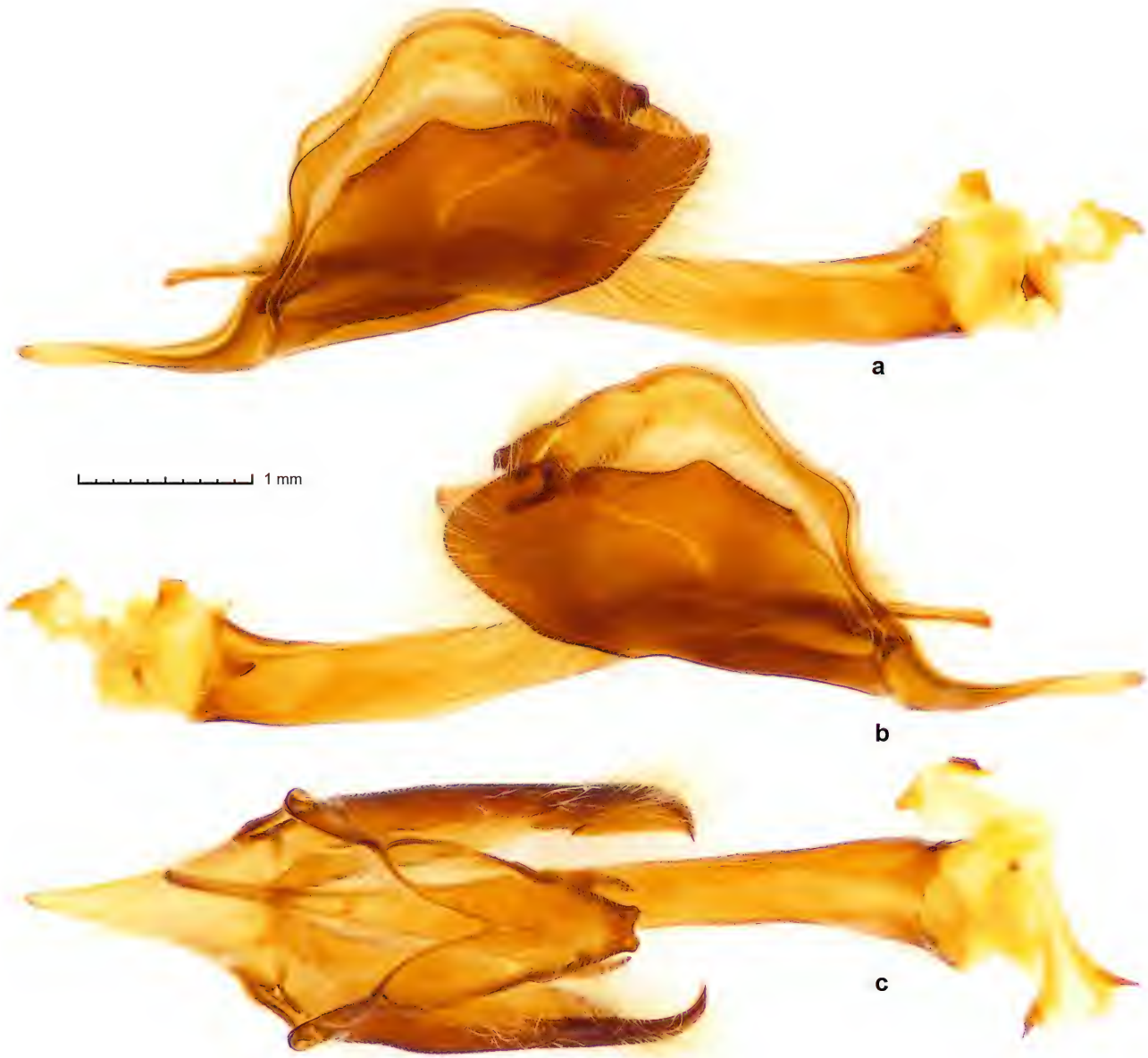


Fig. 138. Male genitalia of *Vacerra saltina* **sp. n.** holotype NVG-23045D07 (data in text) in different views: **a)** left lateral, **b)** right lateral, and **c)** dorsal.

19 | km 28-30, 650-750 | m 17-ix-89 Leg R | Eisele 89S3], [Vacerra hermesia | cecropterus (M) | Det Robert Eisele | ii-10], [MGCL Accession | #2011-4 | Robert Eisele], [DNA sample ID: | NVG-23045D07 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24065B11 | c/o Nick V. Grishin], [genitalia: | NVG241111-19 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Vacerra saltina | Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection. **Paratypes:** 2♂♂ NVG-24065B12 & NVG-24065C01 and 1♀ NVG-23045D08, data as the holotype but km. 6–8, nr. Quebrada del Remanso, 450 m, 20-May-1977.

Type locality. Argentina: Salta Province, Orán, km 28–30 of Rt. 19 Agua Blanca to Angosto, elevation 650–750 m.

Etymology. The name is a fusion of *Salt*[a] + [Argent]*ina* for the type locality of this species and is treated as a feminine noun in apposition.

Distribution. Currently known only from northern Argentina.

Vacerra cuza Grishin, new species

http://zoobank.org/5BFDC6C4-DAA3-446D-B9DF-E2BA2D270F56

(Figs. 134 part, 139–140)

Definition and diagnosis. Genomic sequencing of a specimen from Cuzco, Peru, identified as "*Vacerra hermesia cecropterus*" reveals that it is not monophyletic with the lectotype of *Vacerra cecropterus* (Draudt, 1923), **stat. rest.** (type locality in Bolivia: Rio Zongo, sequenced as NVG-18093D10) and is instead sister to *Vacerra hermesia* (Hewitson, 1870) (type locality in Ecuador), being genetically differentiated from them at the species level (Fig. 134); e.g., their COI barcodes differ by 2.0% (13 bp) (from its sister *V. hermesia*) and 1.5% (10 bp) (from a more distant relative *V. cecropterus*). Therefore, the Peruvian specimens represent a new species. This new species keys to "*Vacerra hermesia cecropterus*" (O.8.7.(b)) in Evans (1955) but differs from its relatives by a combination of the following characters: green dorsal overscaling typically subdued, does not strongly stand out and is more olive-brown (not prominently blue-green as in *V. hermesia*); the hyaline spot in the forewing cell CuA_1-CuA_2 being more rounded and strongly separated from the discal cell spot by a brown ground color area and offset distad from it; a small but prominent cream-colored spot in the discal cell of the ventral hindwing; traces of postdiscal cream-colored spots in ventral hindwing cells CuA_1-CuA_2 and CuA_2-1A+2A and at the base of cell Sc+R_1-RS; and a size comparable to *V. cecropterus* and smaller than *V. hermesia*. Due to the cryptic nature of this species, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly6841.81.1:T529A, aly6841.81.1:C564T, aly84.83.1:G822A, aly36444.1.1:G117A, aly36444.1.1:C141T, aly1603.41.2:A72A (not C), aly16812.3.4:C81C (not T), aly16812.3.4:G174G (not T), aly164.16.14:G66G (not C), aly164.16.14:C195C (not T); and COI barcode: T19C, T121C, T250C, T361T, T385C, T436C.

Barcode sequence of the holotype. Sample NVG-18128C01, GenBank PV550061, 658 base pairs:

AACTTTATATTTTATTTTCGGTATTTGAGCAGGAATACTAGGAACTTCACTAAGACTTTTAATTCGTACAGAATTAGGTAATCCAGGATCTTTAATTGGAGACGATCAAATTTATAATACC
ATTGTCACAGCTCATGCTTTTATTATAATTTTCTTTATAGTTATACCAATTATAATCGGAGGATTTGGAAATTGATTAGTTCCTCTTATATTAGGAGCTCCAGATATAGCTTTCCCACGAA
TAAATAACATAAGATTTTGAATATTACCCCCATCATTAACATTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACCGGTTGAACTGTTTATCCACCTTTATCTTCAAATATTGC
CCATCAAGGAGCTTCTGTTGACTTAGCAATTTTTTCTCTTCATTTAGCTGGTATTTCTTCTATTTTAGGAGCCATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTTGTTTGATCTGTAGGTATTACAGCTTTATTATTACTTTTATCTTTACCTGTTTTAGCTGGAGCAATTACCATATTACTCACTGATCGAAATTTAAATACTT
CATTTTTTGATCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT

Type material. Holotype: ♂ currently deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 139 (genitalia Fig. 140), bears the following seven printed (text in italics handwritten) rectangular labels, six white: [Peru: Cuzco Dept, 1375m | Cosñipata Valley, San Pedro | 13° 03' S, 71° 33' W | November 3, 2017 | Leg: W. Dempwolf], [Vacerra hermesia | cecropterus | ♂ | Coll of: W R Dempwolf], [DNA sample ID: | NVG-18128C01 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24015G02 | c/o Nick V. Grishin], [genitalia: | NVG241114-46 | c/o Nick V. Grishin], [WRD 14,869], and one red [HOLOTYPE ♂ | Vacerra cuza | Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the abdomen prior to genitalia dissection.

Fig. 139. *Vacerra cuza* **sp. n.** holotype ♂ NVG-18128C01 in dorsal (left) and ventral (right) views, data in text.

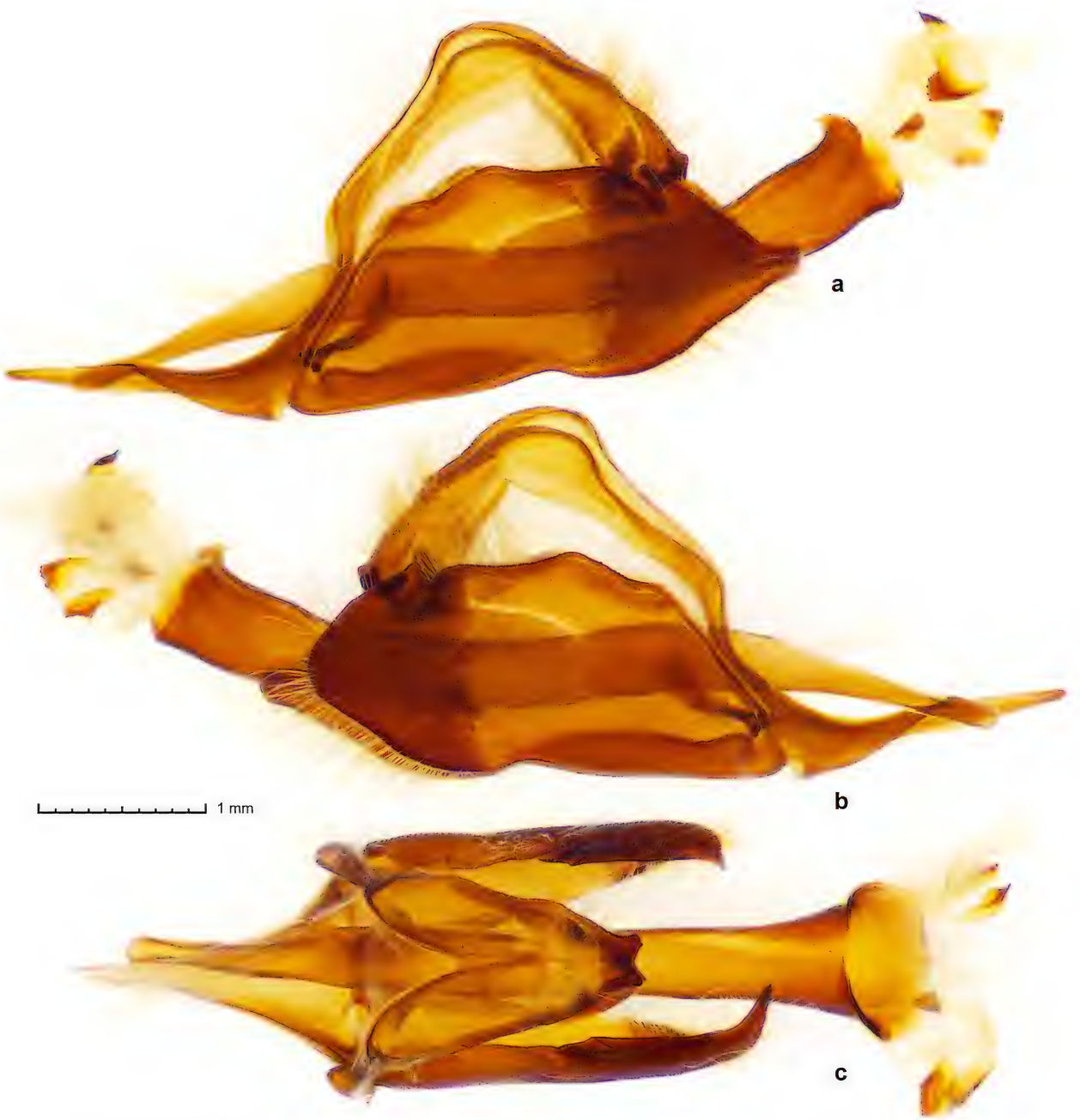


Fig. 140. Male genitalia of *Vacerra cuza* **sp. n.** holotype NVG-18128C01 (data in text) in different views: **a)** left lateral, **b)** right lateral, and **c)** dorsal.

Type locality. Peru: Cuzco Region, Cosñipata Valley, San Pedro, elevation 1375 m, GPS −13.05, −71.55.

Etymology. The name is formed from the name of the Peruvian region with the type locality and is treated as a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in Cuzco, Peru.

Oligoria (*Oligoria*) *tinalandia* Grishin, new species

http://zoobank.org/DEA84675-0EF3-454E-A754-C848A69F0F63

(Figs. 141 part, 142)

Definition and diagnosis. A specimen from the western slopes of the Andes in northern Ecuador is sister to *Oligoria* (*Oligoria*) *rindgei* (H. Freeman, 1969) (type locality in Mexico: Oaxaca), but is genetically

differentiated from it at the species level (Fig. 141); e.g., their COI barcodes differ by 3.6% (24 bp), and, therefore, represents a new species. This new species keys to "*Decinea percosius*" (L.11.7) in Evans (1955) and, while being most similar to its sister *O. rindgei*, differs from it and other relatives by the following combination of characters in females: hyaline spots are larger than in *O. rindgei*, three forewing subapical spots are increasing in length from the costal margin, more rectangular (less rounded) spots in cells M_3-CuA_1 and CuA_1-CuA_2, two pale spots on both sides of the hindwing, the anterior spot is semi-hyaline and larger than the posterior one, a small pale spot at the end of the discal cell on the ventral hindwing, other pale markings are less developed than *O. rindgei*, tornal cream-colored area on ventral forewing is less developed, more overscaled with brown in the anterior part of the cell CuA_2-1A+2A, discal cell cream spot on ventral hindwing is less developed, ventral hindwing is with paler submarginal overscaling from the tornus to the CuA_2 vein. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly522.8.3:G69A, aly1041.8.1:C42A, aly2178.47.6:G90A, aly168.10.2:G207A, aly3936.4.11:C24G, aly1080.19.1:G111G (not A), aly1468.7.9:T72T (not C), aly525.127.2:G277G (not A), aly84.86.1:A81A (not T), aly37338.52.1:A45A (not C); and COI barcode: T22C, A100G, T163T (not C), T367C, T403C, T571C.

Barcode sequence of the holotype. Sample NVG-24065F10, GenBank PV550062, 658 base pairs:

AACTTTATATTTTATTTTTGGCATTTGAGCAGGAATATTAGGAACTTCCTTAAGATTATTAATTCGAACAGAATTAGGTAATCCAGGATCATTAATTGGGAATGACCAAATTTATAATACT
ATTGTCACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATATTAGGAGCTCCTGATATAGCTTTCCCACGAA
TAAATAATATAAGATTTTGAATATTACCTCCTTCTTTAATTCTATTAATTTCAAGAAGAATTGTAGAAAATGGAGCTGGAACTGGTTGAACAGTTTATCCCCCTTTATCTTCTAATATTGC
CCACCAAGGATCCTCTGTTGATTTAGCAATTTTTTCTCTCCATTTAGCTGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAAAAATTTATCA
TTTGATCAAATACCTTTATTTGTATGATCTGTAGGTATTACTGCTTTATTATTACTTTTATCTTTACCTGTTTTAGCTGGAGCTATCACTATATTACTTACTGATCGAAATCTTAATACTT
CATTTTTTGATCCAGCAGGAGGAGGGGATCCAATTTTATACCAACATTTATTT

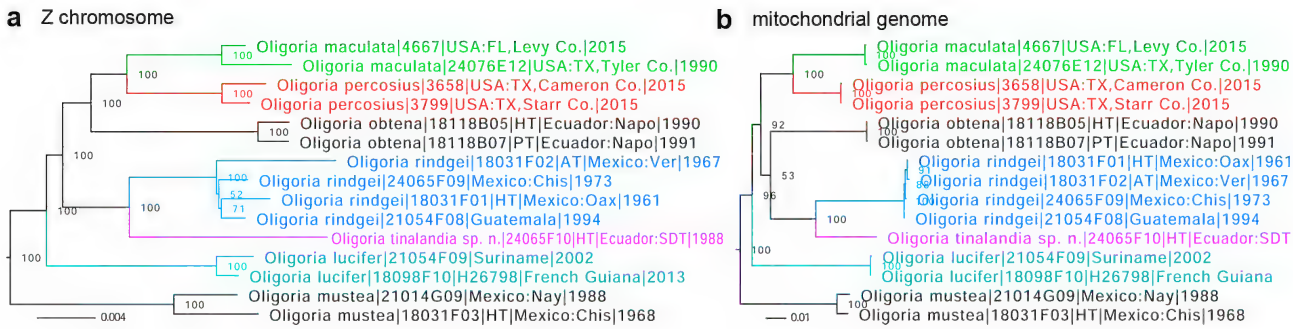


Fig. 141. Phylogenetic trees of *Oligoria* (*Oligoria*) species constructed from protein-coding regions in: **a)** the Z chromosome, based on 414,570 positions, and **b)** the mitochondrial genome: *O. maculata* (W. H. Edwards, 1865) (green), *O. percosius* (Godman, 1900) (red), *O. rindgei* (blue), *O. tinalandia* **sp. n.** (magenta), and *O. lucifer* (Hübner, [1831]) (cyan). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes.

Fig. 142. *Oligoria* (*Oligoria*) *tinalandia* **sp. n.** holotype ♀ NVG-24065F10 in dorsal (left) and ventral (right) views.

Type material. Holotype: ♀ deposited in the McGuire Center for Lepidoptera and Biodiversity Collection, Gainesville, FL, USA (MGCL), illustrated in Fig. 142, bears the following seven printed (text in italics handwritten) rectangular labels, six white: [ECUADOR | Pichincha Province | Hotel Tinalandia | 12 km E Santa | Domingo de los | Colorados | 750–850 m | 11 May 1988 | leg C&A Austin], [Allyn Museum Photo | No. *901017A-17,18*], [Genitalia Vial | SRS-*3829*], [*Decinea percosius ?* | *(Godman)* ♀ | det. S. R. Steinhauser], [G.T. Austin colln. | MGCL Accession | #2004-5], [DNA sample ID: | NVG-24065F10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♀ | Oligoria (Oligoria) | tinalandia Grishin]. Genitalia vial was not located in the collection, but a vial with genitalia from a different specimen was pinned next to the holotype.

Type locality. Ecuador: Santo Domingo de los Tsáchilas Province, 12 km east of Santo Domingo de los Tsáchilas, Tinalandia Lodge, elevation 750–850 m.

Etymology. The name is given for the type locality and is a feminine noun in apposition.

Distribution. Currently known only from the holotype collected in the western Andes of Northern Ecuador.

Eutychide trombella Grishin, new species

http://zoobank.org/8CAB42B4-0856-4160-8AD1-ECFE68D36540

(Figs. 143 part, 144)

Definition and diagnosis. Sister to all known *Eutychide* Godman, 1900 (type species *Hesperia physcella* Hewitson, 1866) in the genomic trees (Fig. 143), this female was identified as a possible *Tromba xanthura* (Godman, 1901) (type locality Panama: Bugaba) due to superficial similarities. This new species keys (incompletely) to *Eutychide paria* (Plötz, 1882) (J.50.5) in Evans (1955) but differs from it and other relatives by females having paler brown to yellow submarginal areas on the ventral hindwing, gradually getting paler towards the outer margin, and lacking pale or hyaline spots, except a minute semi-hyaline spot in the forewing cell M_2-CuA_1, otherwise brown with paler fringes on the hindwing and towards the tornus of the forewing, as *E. paria* but fringes have a stronger orange tint. This species is not cryptic and is identifiable by its phenotype. In DNA, a combination of the following base pairs is diagnostic in the

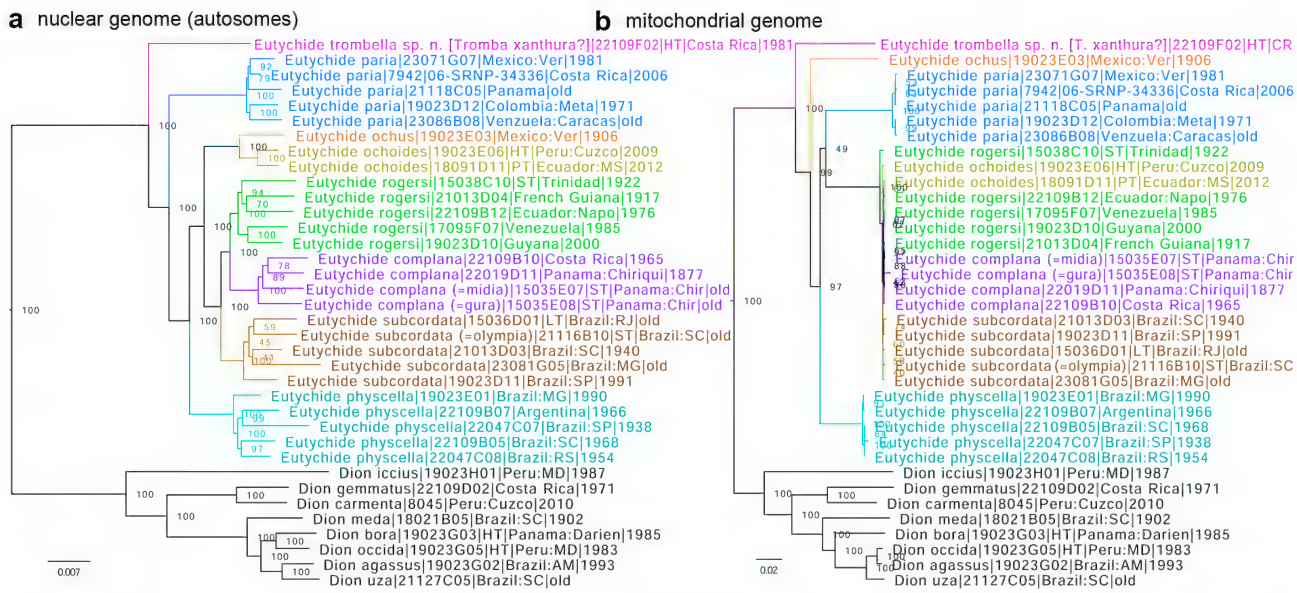


Fig. 143. Phylogenetic trees of *Eutychide* and its sister *Dion* Godman, 1901 constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 4,780,623 positions, and **b)** the mitochondrial genome. Different *Eutychide* species are colored differently: *E. trombella* **sp. n.** (magenta), *E. paria* (blue), *E. ochus* Godman, 1900 (orange), *E. ochoides* Grishin, 2023 (olive), *E. rogersi* (Kaye, 1914) (green), *E. complana* (Herrich-Schäffer, 1869) (purple), *E. subcordata* (Herrich-Schäffer, 1869) (brown), and *E. physcella* (Hewitson, 1866) (cyan). Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. Note the mitochondrial genome introgression among four species, which, as a result, cannot be identified using COI barcodes.

Fig. 144. *Eutychide trombella* **sp. n.** holotype ♀ NVG-22109F02 in dorsal (left) and ventral (right) views, data in text.

nuclear genome: aly536.107.1:C90A, aly536.107.1:C114T, aly536.107.1:T144C, aly5412.7.12:T78C, aly347.13.1:C108T, aly252.18.1:C631C (not A), aly383.4.5:G51G (not A), aly1139.56.27:G42G (not A), aly1139.56.27:C45C (not T), aly527.10.1:A51A (not G); and COI barcode: T46C, A67G, T202T, A214G, A325A, T421C, A607A.

Barcode sequence of the holotype. Sample NVG-22109F02, GenBank PV612660, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGAATATTAGGAACCTCTTTAAGATTACTAATTCGGACAGAATTAGGAAATCCCGGTTCCTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACTGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTCTTATATTGGGAGCACCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATATTACCTCCTTCACTAATATTATTAATTTCAAGAAGAATTGTTGAAAATGGTGCAGGAACAGGATGAACAGTTTACCCCCCACTTTCATCTAATATTGC
TCATCAAGGTTCTTCAGTTGATTTAGCAATTTTTTCTTTGCATTTAGCAGGAATTTCCTCTATTTTAGGAGCTATTAATTTCATTACTACAATTATTAATATACGAATTAGAAATTTATCA
TTTGATCAAATACCCTTATTTGTATGATCCGTAGGTATTACAGCTTTATTATTATTATTATCCTTACCCGTATTAGCAGGAGCAATTACAATACTTTTAACTGATCGAAATTTAAACACCT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♀ deposited in the collection of the California Academy of Sciences, San Francisco, CA, USA (CAS), illustrated in Fig. 144, bears the following six rectangular labels (1st handwritten, others printed with handwritten text shown in italics), five white: [Costa Rica, Cariblanco | Prov. Cuesta Angel | 21 Mar 81, 800 m], [*Tromba* | *xanthura?* | *(Godm.)* | Det.C.D.Macneill'*98*], [Collection of | C.D.MacNeill], [DNA sample ID: | NVG-22109F02 | c/o Nick V. Grishin], [{QR Code} CASENT | 8568789], and one red [HOLOTYPE ♀ | Eutychide | trombella Grishin].

Type locality. Costa Rica: Heredia Province, Cuesta Angel Forest Ravine near Cariblanco, elevation 800 m.

Etymology. The name is given for the phenotypic resemblance of this species with *Tromba* Evans, 1955 (type species *Tromba tromba* Evans, 1955) and is an adjective.

Distribution. Currently known only from the holotype collected in northeastern Costa Rica.

Talides hispina Grishin, new species

http://zoobank.org/C5A26964-A1F4-4601-98D1-1A3FC7583319

(Figs. 145 part, 146–147)

Definition and diagnosis. Genomic analysis of *Talides* Hübner, 1819 (type species *Talides sinois* Hübner, 1819) reveals a specimen from Ecuador sister to *Talides hispa* Evans, 1955 (type locality Panama: Bugaba) that is genetically differentiated from it at the species level (Fig. 145); e.g., their COI barcodes differ by 2.9% (19 bp). Therefore, this specimen represents a new species. This new species keys to "*Talides alternata hispa*" (K.13.3(b)) in in Evans (1955) but differs from its relatives by a combination of the following characters: the harpe is nearly straight at the dorsal margin and the process of the tegumen is nearly reaching the end of the uncus; the hindwing is less rounded, with orange fringes; two subapical hyaline spots on forewing closest to the costa are dot-like much smaller than the third spot (about a quarter of its size) and are offset basad from it. Due to the cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly728.7.2:C312G, aly728.7.2:A316C, aly577.

59.7:T621C, aly2633.1.7:T471A, aly2633.1.7:A486T, aly127.44.3:C1029C (not T), aly318.28.4:C189C (not T), aly4506.4.2:A66A (not G), aly2627.2.5:G60G (not A), aly5719.4.7:C84C (not A); and COI barcode: T205C, T250T, C282T, T386C, C467A, 574C.

Barcode sequence of the holotype. Sample NVG-23069C01, GenBank PV550063, 658 base pairs:

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATTAGGAACTTCTCTAAGATTATTAATTCGAACAGAATTAGGTAACCCAGGATTTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTAACAGCTCACGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCCCTTATACTTGGAGCTCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTCTGAATGCTTCCCCCCTCTTTAATATTATTAATTTCAAGAAGAATTGTAGAAAATGGTGCTGGTACTGGATGAACTGTATACCCCCCCCTTTCAGCAAATATTGC
CCACCAAGGTTCTTCTGTTGATCTAGCAATTTTTTCTCTTCATTTAGCAGGAATTTCCTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATAAAAATTAAAAATTTATTA
TTTGATCAAATACCCTTATTTGTATGATCTGTAGGAATTACAGCTTTATTATTATTACTATCTTTACCTGTTTTAGCAGGAGCTATTACCATACTTCTTACAGATCGTAATTTAAATACTT
CATTTTTTGATCCTGCAGGTGGAGGAGACCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU), illustrated in Fig. 146 (genitalia Fig. 147), bears the following five printed (text in italics handwritten) rectangular labels, four white: [ECUADOR: Napo Prov. | Misahualli (Lodge & vic.) | 1.03381°S, 77.66191°W | VII-5-10-2010, C.M.Riley], [DNA sample ID: | NVG-23069C01 | c/o Nick V. Grishin], [DNA sample ID: | NVG-24015D06 | c/o Nick V. Grishin], [genitalia: | NVG241114-01 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Talides | hispina Grishin]. The first DNA sample (sequenced) refers to the extraction from a leg and the second (stored) is from the tip of the abdomen prior to genitalia dissection.

Type locality. Ecuador: Napo Province, vicinity of Misahualli Lodge, GPS −1.03381, −77.66191.

Etymology. The name is formed from its sister species, *T. hispa*, which is made longer to indicate a more southern distribution of the new species. The name is a noun in apposition.

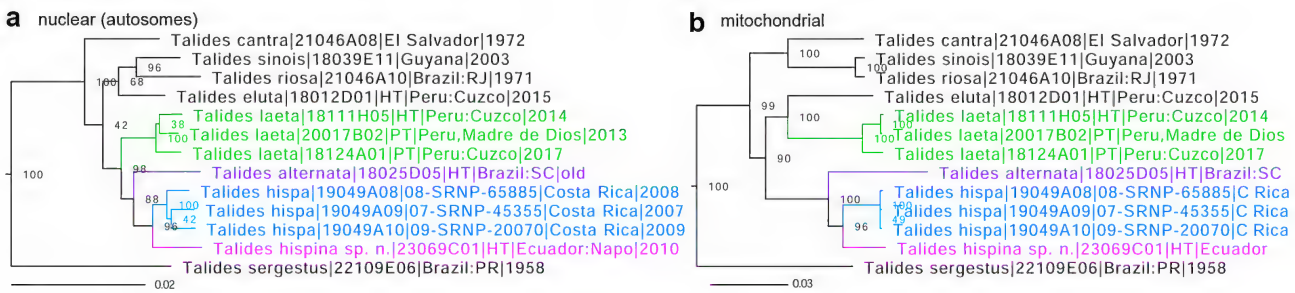


Fig. 145. Phylogenetic trees of *Talides* constructed from protein-coding regions in: **a)** the nuclear genome (autosomes) and **b)** the mitochondrial genome: *T. hispina* **sp. n.** (magenta), *T. hispa* (blue), *T. alternata* E. Bell, 1941 (purple), and *T. laeta* Grishin, 2023 (green).

Fig. 146. *Talides hispina* **sp. n.** holotype ♂ NVG-23069C01 in dorsal (left) and ventral (right) views, data in text.

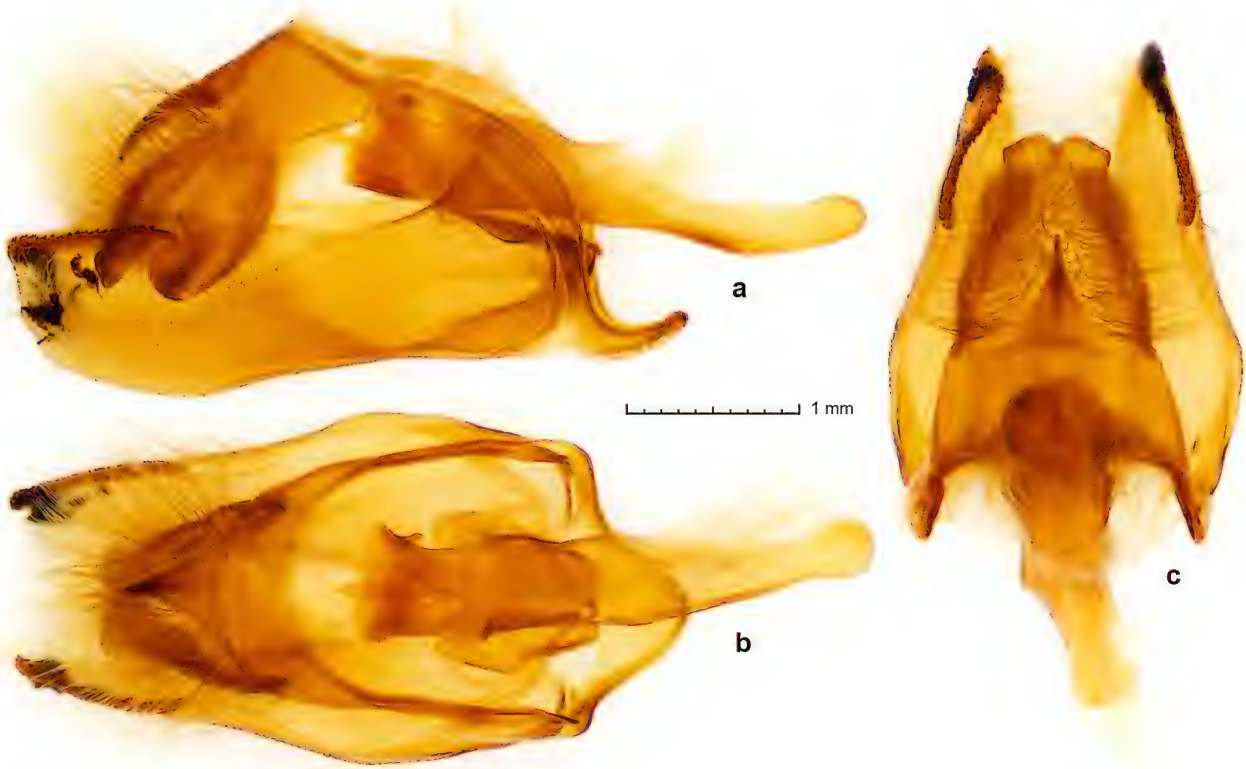


Fig. 147. Male genitalia of *Talides hispina* **sp. n.** holotype NVG-23069C01 in different views, data in text: **a)** right lateral, **b)** anterodorsal, and **c)** dorsal.

Distribution. Currently known only from the holotype collected in northern Ecuador.

Comment. Genitalic harpes have black stains, a sign of possible damage during or right after eclosion.

Lectotype designations and comments on the type localities of the taxa in the *Damas clavus* (Herrich-Schäffer, 1869) complex

Currently, the following eight available names are regarded as junior subjective synonyms of *Goniloba clavus* Herrich-Schäffer, 1869 (type locality not specified): *Goniloba corope* Herrich-Schäffer, 1869 (type locality not specified), *Carystus orope* Capronnier, 1874 (Plötz in litt.) (type locality includes at least Botafogo, Rio de Janeiro, Brazil), *Hesperia crataea* Hewitson, 1876 (type locality in Brazil: Bahia), *Proteides cervus* Möschler, 1877 (type locality in Suriname), *Hesperia angulis* Plötz, 1886 (type locality in Panama), *Proteides ampyx* Mabille, 1891 (type locality in Panama), *Thracides polles* Godman, 1901 (type locality in Nicaragua, Panama, and Brazil), and *Perichares tripuncta* Draudt, 1923 (type locality stated as South Brazil on the label of the lectotype). To gain further insights into the relationships between these taxa, we located primary type specimens of all but one of them. While *P. tripuncta* is already represented by the lectotype, others are syntypes, and we designate lectotypes for six names in this section and one in the next.

To stabilize nomenclature and define the name *Goniloba clavus* Herrich-Schäffer, 1869 (type locality not specified) objectively, N.V.G. hereby designates a syntype in the MFNB collection, a female that bears the following ten rectangular labels (1st purple, others white; 2nd, 3rd, 5th, and 7th handwritten, others printed: [Origin.], [clavus HS.], [Col. Staudinger | K. 669], [Coll. H.—Sch.] (a large X is penciled across "—" on this label), [917.], [Coll. | Staudinger], [Prot.| Clavus | HS.], [Clavus | H-Sch.], [{QR Code} http://coll.mfn-berlin.de/u/ | 449fc1], [DNA sample ID: | NVG-15036D06 | c/o Nick V. Grishin] as the **lectotype** of *Goniloba clavus* Herrich-Schäffer, 1869. The 2nd and 7th labels are likely written by Plötz and Staudinger, respectively. The lectotype is missing the tornal section of its left

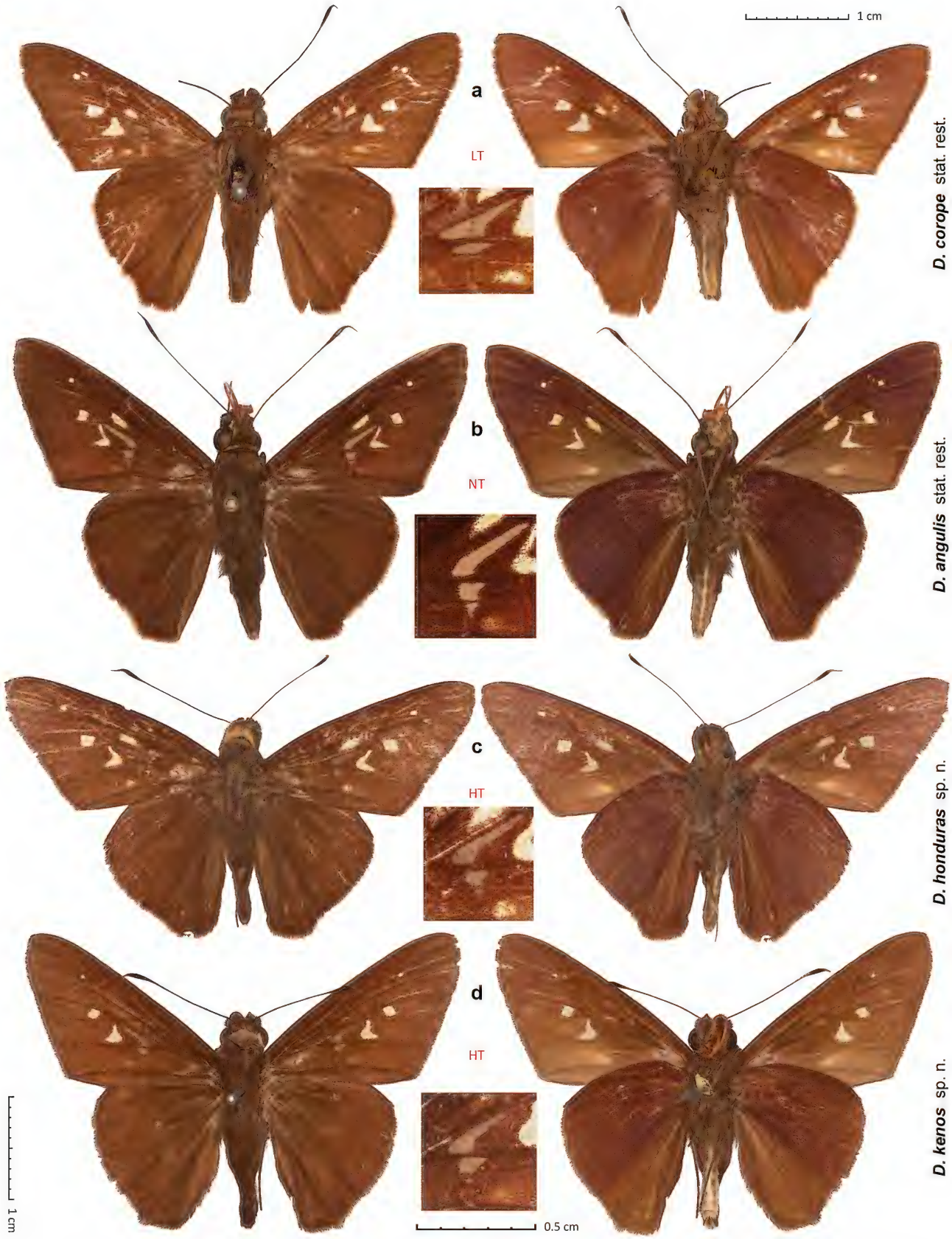


Fig. 148. Primary type specimens of *Damas* in dorsal (left) and ventral (right) views, data in text: **a)** lectotype of *D. corope* **stat. rest.**, **b)** neotype of *D. angulis* **stat. rest.**, **c)** holotype of *D. honduras* **sp. n.**, and **d)** holotype of *D. kenos* **sp. n**. Insets show magnified (scale indicated by 0.5 cm bar) middle of forewing with digitally enhanced stigma of each specimen.

Fig. 149. Male genitalia of *Damas*, data in text: **a–d)** lectotype of *D. corope* **stat. rest.**, left valva detached, aedeagus not shown; **e–g)** specimen of *D. angulis* **stat. rest.** NVG-23123B02, left valva detached; **h–i)** paratype of *D. honduras* **sp. n.** NVG-23123A10; **j–k)** paratype of *D. kenos* **sp. n.** NVG-23123B06; and **l–m)** paratype of *D. lavandas* **sp. n.** NVG-24099C06. Views: **b**, **e**, **h**, **j, m)** left lateral, **a**, **d**, **g)** right lateral, **c**, **f**, **i**, **k, l)** dorsal, **d)** shows caudal part of the left valva.

hindwing and has a deep tear from the middle of the right forewing outer margin. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). Genomic sequencing places the lectotype among specimens from Southeast and South Brazil (Fig. 152), suggesting that the type locality of *G. clavus* is in this region. The COI barcode sequence of the lectotype, sample NVG-15036D06, GenBank PV550065, 658 base pairs, is:

AACTCTATATTTTATTTTTGGTATCTGAGCAGGATTATTAGGAACTTCTTTAAGTATATTAATTCGAACAGAATTAGGAAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTAACAGCTCATGCCTTTATTATAATTTTCTTTATAGTTATACCTATTATAATTGGGGGATTTGGTAACTGATTAGTACCTTTAATGTTAGGAGCTCCTGATATAGCTTTTCCTCGAA
TAAATAATATAAGATTCTGAATATTACCCCCATCATTAGTCTTGCTAATTTCAAGAAGAATTGTAGAAACTGGAGCAGGAACTGGTTGAACTGTTTACCCCCCTCTTTCTTCCAATATTGC
TCATCAAGGAGCTTCGGTAGATTTAGCTATTTTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATTAATTTTATTACTACAATCATTAATATACGTGTAAGAAATTTATTA
TTTGATCAAATACCTTTATTTATTTGATCTGTAGGAATTACAGCCCTCTTATTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAATCTTAATACTT
CTTTTTTTGACCCAGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

To stabilize nomenclature and define the name *Goniloba corope* Herrich-Schäffer, 1869 (type locality not specified) objectively, N.V.G. hereby designates a syntype in the MFNB collection, a male illustrated in Fig. 148a (genitalia Fig. 149a–d) that bears the following eight rectangular labels (1st red, 2nd purple, others white; 4th and 6th handwritten, others printed with handwritten text shown in italics): [Lectotypus], [Origin. | *Corope* | *HS.*], [Coll. H.—Sch.], [Proteid. | corope | HS.], [Coll. | Staudinger], [Corope | H-Sch.], [{QR Code} http://coll.mfn-berlin.de/u/ | 3226a4], [DNA sample ID: | NVG-15035A04 | c/o Nick V. Grishin] as the **lectotype** of *Goniloba corope* Herrich-Schäffer, 1869. Handwriting on the 2nd and 4th labels matches that of Staudinger. The lectotype is missing half of its left antenna, its right wings are set farther apart from each other than the left wings, and both forewings have tears at the outer margin. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). Genomic sequencing places the lectotype among specimens from Suriname (Fig. 152), suggesting that the type locality of *G. corope* is in the Amazonian region, likely in Suriname.

To stabilize nomenclature and define the name *Hesperia crataea* Hewitson, 1876 (type locality in Brazil: Bahia) objectively, N.V.G. hereby designates a syntype in the BMNH collection, a male that bears the following four labels (1st round with a red circle, others rectangular; 2nd red, others white; 3rd handwritten by Hewitson, 2nd contains no text, others printed with handwritten text shown in italics): (Type) with (H | 2335) handwritten on the other side of this label, [ ], [crataea], [*Bahia.* | Hewitson Coll. | 79—69. | Hesperia | *crataea. 1.*] as the **lectotype** of *Hesperia crataea* Hewitson, 1876. The lectotype is missing its abdomen, has some damage along the outer margin of the right hindwing towards the tornus, and is pinned on a short pin inserted into a holder pinned on a regular pin. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024).

To stabilize nomenclature and define the name *Proteides cervus* Möschler, 1877 (type locality in Suriname) objectively, N.V.G. hereby designates a syntype in the MFNB collection, a female that bears the following eight rectangular labels (1st purple, 2nd and 3rd green, others white; 2nd, 3rd, and 5th handwritten, others printed): [Origin.], [Surinam. | Bgdl. | L. 74.], | [Type. | Verhdlg. d. zool. bot. | Gsllschft. Wien. | XXVI.T.IV.17.p.333.], [Coll. Möschl.], [Cervus | Möschl], [Coll. | Staudinger], [{QR Code} http://coll.mfn-berlin.de/u/ | 44a014], [DNA sample ID: | NVG-15036F09 | c/o Nick V. Grishin] as the **lectotype** of *Proteides cervus* Möschler, 1877. The lectotype is missing its antennae, the end of the abdomen, and the apex of the right hindwing, which was repaired and the middle section glued on, leaving a gap in the middle. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The type locality of *P. cervus* (as given on the label) is Suriname: Brokopondo District, Berg en Dal (abbreviated as "Bgdl."). The COI barcode sequence of the lectotype, sample NVG-15036F09, GenBank PV550066, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTATATGAGCAGGATTGTTAGGAACTTCATTAAGTATATTAATTCGAACAGAATTAGGAAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCTTTAATATTAGGTGCTCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGGATACTACCCCCATCCTTAATCTTATTAATTTCAAGAAGAATCGTAGAAACTGGAGCAGGAACTGGTTGAACTGTTTATCCCCCTCTTTCCTCCAATATCGC
TCACCAAGGAGCTTCAGTAGATTTAGCTATTTTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATTAATTTTATTACTACAATCATTAATATACGAGTAAGAAACTTATCC
TTTGATCAAATACCATTATTTATTTGATCAGTAGGAATTACAGCTCTCTTATTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAATCTTAATACTT
CTTTTTTCGATCCAGCTGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

To stabilize nomenclature and define the name *Proteides ampyx* Mabille, 1891 (type locality in Panama: Chiriquí) objectively, N.V.G. hereby designates a syntype in the MFNB collection, a male that bears the following eight rectangular labels (1st purple, others white; 2nd, 3rd, 4th, and 6th handwritten,

others printed): [Origin.], [Chiriqui | Tr.], [Pr. Ampyx | Mb], [Proteid. | Ampyx | Mab.], [Coll. | Staudinger], [Ampÿx | Mab.], [{QR Code} http://coll.mfn-berlin.de/u/ | 449fc0], [DNA sample ID: | NVG-15036D05 | c/o Nick V. Grishin] as the **lectotype** of *Proteides ampyx* Mabille, 1891. According to its 2nd label, the lectotype was collected in Panama: Chiriquí by Troetsch. The 3rd and the 4th labels are likely written by Mabille and Staudinger, respectively. The lectotype has scales rubbed off at the base of the right hindwing beneath, which was re-attached, and two angular bends in its left antenna. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). The COI barcode sequence of the lectotype, sample NVG-15036D05, GenBank PV550067, 658 base pairs, is:

AACTTTATATTTTATTTTCGGTATATGAGCAGGATTATTAGGAACTTCCTTAAGTATATTAATTCGAACAGAATTAGGAAATCCCGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAACTGATTAGTACCTTTAATATTAGGTGCTCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGGATACTACCCCCATCCTTAATCTTATTAATTTCAAGAAGAATCGTAGAAACTGGAGCAGGAACTGGTTGAACTGTTTACCCCCCCCTTTCATCCAATATTGC
TCACCAAGGAGCTTCAGTAGATTTAGCTATTTTTTTCTCTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATCAATTTTATTACCACAATTATTAATATACGAGTAAGAAATTTATCC
TTTGATCAAATACCATTATTTATTTGATCCGTAGGAATTACAGCTCTCTTATTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAACCTTAATACTT
CTTTTTTTGACCCAGCTGGTGGAGGAGATCCTATTTTATACCAACATTTATTT

To stabilize nomenclature, to define the name *Thracides polles* Godman, 1901 (type locality in Nicaragua, Panama, and Brazil) objectively, and narrow down the type locality, N.V.G. hereby designates a syntype in the MFNB collection, a female that according to its label was figured on the plate 105 in the original publication (Godman 1901) and bears the following nine rectangular labels (1st purple, others white; 4th handwritten, others printed): [Origin.], [Chiriqui], [811.], [P. b. 159:12.], [Coll. | Staudinger], [Sp. figured], [B.C.A.Lep.Rhop. | Thracides | polles, | Godm.], [{QR Code} http://coll.mfn-berlin.de/u/ | 440fc9], [DNA sample ID: | NVG-15036E01 | c/o Nick V. Grishin] as the **lectotype** of *Thracides polles* Godman, 1901. The lectotype is missing the left antenna and has two small tears at the outer margins of the left hindwing along CuA_2 vein and the right forewing in the cell CuA_1-CuA_2, but otherwise is a specimen in excellent condition. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). As a result of the lectotype designation, the type locality of *T. polles* becomes Panama: Chiriquí. The COI barcode sequence of the lectotype, sample NVG-15036E01, GenBank PV550068, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTGTATGAGCAGGATTATTAGGAACTTCCTTAAGTATACTAATTCGAACAGAATTAGGAAATCCTGGATCTTTAATTGGAGACGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAACTGATTAGTACCTTTAATATTAGGTGCTCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGGATACTACCCCCATCCTTAATCTTATTAATTTCAAGAAGAATCGTAGAAACTGGAGCAGGAACTGGTTGAACTGTTTACCCCCCCCTTTCATCCAATATTGC
CCACCAAGGGGCTTCAGTAGATTTAGCTATTTTTTTCTCTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATCAATTTTATTACCACAATTATTAATATACGAGTAAAAAATTTATCC
TTTGATCAAATACCATTATTTATTTGATCCGTAGGAATTACAGCTCTCTTATTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAACCTTAATACTT
CTTTTTTTGATCCAGCTGGCGGAGGAGATCCTATTTTATATCAACATTTATTT

Carystus orope Capronnier, 1874 (Plötz in litt.) is a junior subjective synonym of *Tigasis corope* (Herrich-Schäffer, 1869), not of *Damas corope* (Herrich-Schäffer, 1869)

We translate from French the entire original description of *Carystus orope* Capronnier, 1874 (Plötz in litt.) as: "156. **C. Orope,** Plötz. Herrich-Schäffer gave to this species the name of *Gon. Corope*, and to another, the name of *Cobalus Corope*. Mr. Plötz finds that two similar names in the same family are a cause of confusion, and, to avoid it, he suggests for the species in question the name of *Orope*. Sept., 18. Botafogo" (Capronnier 1874). The two species mentioned in the description are *Goniloba corope* Herrich-Schäffer, 1869 (type locality likely in the Amazonian region, lectotype sequenced as NVG-15035A04), currently in the genus *Damas* Godman, 1901 (type species *Goniloba clavus* Herrich-Schäffer, 1869), and *Cobalus corope* Herrich-Schäffer, 1869 (type locality likely in Southeast or South Brazil, syntypes sequenced as NVG-15035A02 and NVG-15035A03), currently in the genus *Tigasis* Godman, 1900 (type species *Tigasis zalates* Godman, 1900). We argue that the original description contains a lapsus and Capronnier should have written "Herrich-Schäffer gave to this species the name of *Cobalus Corope*, and to another, the name of *Gon. Corope*," demonstrating that the two identical species epithets are confusing.

First, the type series of *Carystus orope* includes not only the specimen(s) collected by van Volxem on September 18, 1872, in Botafogo, Rio de Janeiro, Brazil, and listed explicitly by Capronnier (1874), but also specimens that Plötz considered to be *orope*, because Plötz is explicitly mentioned in the description, and the name is attributed to him (Capronnier 1874). Second, in the unpublished manuscript by Plötz (in ZSMC) dated 1876 that served as a draft of his publications, he refers to "*Orope* m.", where

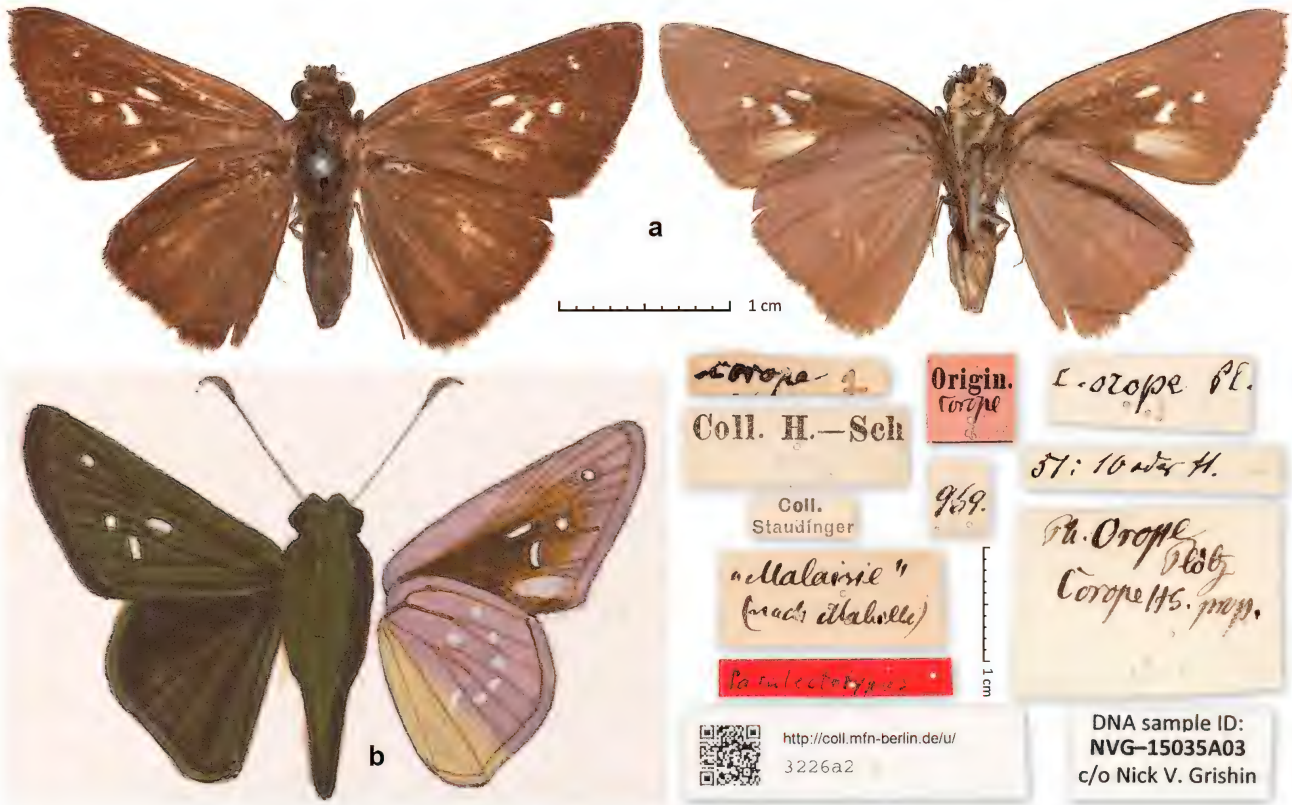


Fig. 150. *Carystus orope* in dorsal (left) and ventral (right) views: **a)** the lectotype of *C. orope* with it labels, labels are reduced by a third compared to the specimen: a smaller scale bar (placed vertically among labels) refers to labels; **b)** Godman's copy of an unpublished illustration t. 533 by Plötz photographed by N.V.G., © The Trustees of the Natural History Museum London made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/).

"m." is for "mihi" ("of me" in Latin), appended to the species name to indicate authorship of the description, in agreement with Capronnier (1874) who attributed the name *orope* to Plötz. Both the manuscript and the published version (Plötz 1882a) list the name "*Corope* HS." ("HS." is for Herrich-Schäffer) under *Orope*, suggesting that *Orope* and at least part of Herrich-Schäffer's *Corope* type series refer to the same taxon and referencing it as "Prodr. 1869. 80. 37." (in the manuscript) and "Prodr. 1869, p. 80 n. 37. ♀" in the publication. The number 37 refers to *Cobalus corope* (number within *Cobalus*), and *Goniloba corope* is the number 48 (number within *Goniloba*) (Herrich-Schäffer 1869). Page number 80 refers to the page with "37. [*Cobalus*] *corope* HS" in "separate reprints" ("Separatabdrücke") bound as a book (Herrich-Schäffer 1864–1869). Third, Godman's copy of the original drawing t[afel]. 533 by Plötz showing his "*Hesperia orope*" reproduced here as Fig. 150b agrees with his and Herrich-Schäffer's descriptions of *Cobalus corope* and not of *Goniloba corope*. Fourth, in his Catalogue, Kirby (1877) expressed the same opinion that "P. Orope, Plötz, *(Carystus O.)* Ann. E. Belg. XVII. p. 34. (1874.)" (note the reference to Capronnier (1874)) was "*Cobalus (nec Goniloba) Corope*". Fifth, *Goniloba corope* is an Amazonian species (see the section above) not known from Rio de Janeiro. In contrast, *Cobalus corope* is distributed in Southeast and South Brazil, where van Volxem collected at least one of the *Carystus orope* syntypes.

In MFNB, we found and sequenced two syntypes of *Cobalus corope*, a male (NVG-15035A02) and a female (NVG-15035A03). The female (Fig. 150a) agrees well with Plötz's key that specifically mentions a female (possibly meaning that the name *orope* was proposed for a female of Herrich-Schäffer's *Cobalus corope*) and the drawing (Fig. 150b) of "*Hesperia orope*" and, therefore, taking into account the discussion above, is a syntype of *Carystus orope* Capronnier. Moreover, one of the labels of this syntype is "C. orope Pl.", likely written by Mabille. To stabilize nomenclature and define the name *C. orope* objectively, N.V.G. hereby designates this female syntype in MFNB shown in Fig. 150a that bears

the following twelve labels (1st purple, 10th red, others white; 2nd, 4th–8th, and 10th handwritten, others printed with handwritten text shown in italics): [Origin. | *corope*], [corope | ♀], [Coll. H.—Sch |], [969.], [C. orope Pl.], [51: 10 oder 11], [„Malaisie“ | (nach Mabille)], [Pa. Orope | Plötz | Corope HS. prop.], [Coll. | Staudinger], [Paralectotypus], [{QR Code} http://coll.mfn-berlin.de/u/ | 3226a2], [DNA sample ID: | NVG-15035A03 | c/o Nick V. Grishin] as the **lectotype** of *Carystus orope* Capronnier, 1874 (Plötz in litt.). The 2nd label might have been written by Herrich-Schäffer, the 7th and 8th labels and the word “corope” on the 1st label are in Staudinger’s handwriting, and the 5th label is in Mabille’s handwriting. The 6th label “51: 10 oder 11.” gives the numbers for “*P*[*renes*]. *orope*, Plötz” (51: 10) and “*P*[*renes*]. *corope*, Herrich-Schäffer, Prodr. Syst. Lep. p. 76” (51: 11) in Mabille’s catalog (1903), meaning that this specimen was identified as *P. orope* or (“oder” in German) *P. corope* by a curator of the MFNB collection. The lectotype of *Carystus orope* is simultaneously a syntype of *Cobalus corope* Herrich-Schäffer, 1869. The lectotype is missing both antennae, and its left wings are separated from each other by a wider gap than the right wings. Images of this specimen photographed by B. Hermier are shown on the Butterflies of America website (Warren et al. 2024). Genomic comparison suggests that the type locality of *C. orope* (and *Tigasis corope*) is in Southeast or South Brazil. The COI barcode sequence of the lectotype, sample NVG-15035A03, GenBank PV550064, 658 base pairs, is:

AACTCTATATTTTATTTTTGGAATTTGAGCAGGTATACTAGGAACTTCCTTAAGTTTATTAATTCGTACAGAATTAGGAAACCCAGGATCTTTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCATTAATATTAGGTGCCCCAGATATAGCTTTCCCCCGAA
TAAATAACATAAGTTTTTGAATACTACCCCCCTCTTTAATATTATTAATTTCTAGTAGAATTGTAGAAAATGGTGCAGGAACTGGATGAACAGTTTATCCCCCTCTTTCTTCTAATATTGC
TCACCAAGGTTCATCTGTTGATTTAGCTATCTTTTCTCTTCACTTAGCAGGTATTTCTTCTATTTTAGGAGCTATTAATTTTATTACTACAATTATTAATATACGAATTAAAAATTTATCT
TTTGATCAAATACCTTTATTTGTATGATCAGTAGGAATTACTGCATTATTATTACTTTTATCTTTACCTGTACTAGCAGGAGCTATTACTATACTTTTAACAGATCGAAATTTAAATACTT
CCTTTTTTGACCCCGCTGGAGGAGGAGATCCTATTTTATACCAACATTTATTT

Both phenotypic assessment and genomic analysis place *Carystus orope* Capronnier, 1874 (Plötz in litt.) as a junior subjective synonym of *Tigasis corope* (Herrich-Schäffer, 1869), not of *Damas corope* (Herrich-Schäffer, 1869) (Fig. 151).

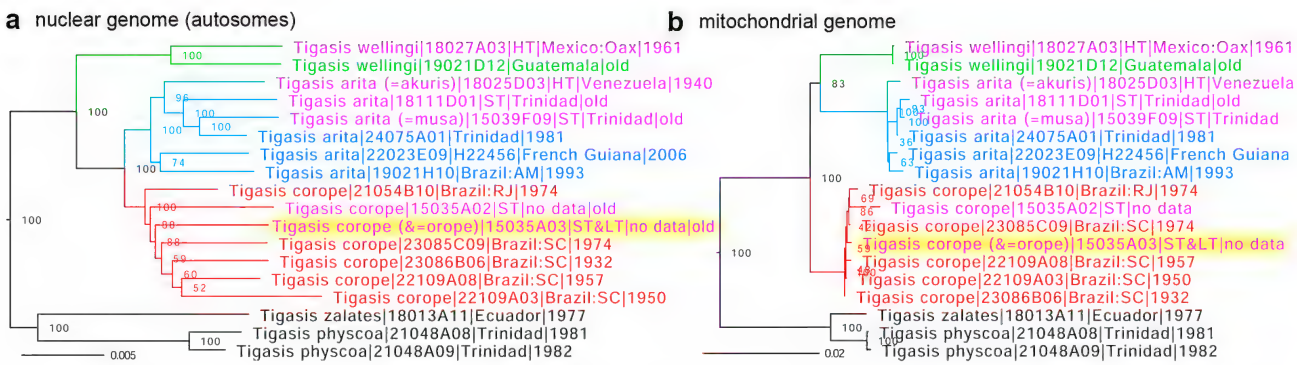


Fig. 151. Phylogenetic trees of selected *Tigasis* species constructed from protein-coding regions in: **a)** the nuclear genome (autosomes), based on 934,104 positions, and **b)** the mitochondrial genome. Different species are colored differently: *T. wellingi* (H. Freeman, 1969) (green), *T. arita* (Schaus, 1902) (blue), and *T. corope* (red). Primary type specimens are labeled in magenta, and the lectotype of *Carystus orope* (which is simultaneously a female syntype of *T. corope*) is highlighted in yellow. Ultrafast bootstrap (Minh et al. 2013) values are shown at nodes. A gap in a branch indicates that a segment of the branch was cut out to reduce its length.

Neotype designation for *Hesperia angulis* Plötz, 1886

Hesperia angulis Plötz, 1886 was described from an unstated number of specimens from Panama collected by Ribbe (Plötz 1886). Our literal translation of the description from German is: “Forewing with a yellow-dusted long hyaline spot on the hind margin of the discal cell, an angle-shaped spot in cell 2, a square spot slightly towards the margin in cell 3, a dot in cell 6, and in cell 1 a dust spot, which is much more extensive on the underside. Otherwise, everything is blackish-brown. The forewing is towards the apex, and the hindwing towards tornus stretched. The antenna is almost 2/3 as long as the forewing. (Ribbe.) 24 mm. Panama.”

Searching for syntypes, we found a specimen in the ZSMC bearing a label “Hesperia Angulis Plötz” in Plötz’s handwriting in addition to the “Lectotypus” label. The lectotype designation has not been

published. This specimen is also labeled as being from "Am. m." (i.e., America Meridionalis, South America, not Panama) and does not have a label connecting it to Carl Ribbe, who collected the type(s) according to the original description. Moreover, this specimen does not fully agree with the original description of *H. angulis*: the hyaline spot in the forewing cell 2 (CuA_1-CuA_2) is crescent-shaped rather than angle-shaped, the latter is characteristic of specimens from Panama, thus supporting the type locality given in the original description. Therefore, we conclude that this specimen is not a syntype, but likely a specimen that was identified by Plötz as *H. angulis*, possibly after the original description. Genomic sequencing of this specimen (NVG-18056H08) places it among specimens collected north of Panama, mainly in Guatemala and southern Mexico, further supporting the hypothesis that it is not a syntype.

Next, we searched for syntypes of *H. angulis* in other collections (see Acknowledgments section for their list), most carefully in the MFNB, where many specimens collected by Ribbe are preserved as part of the Staudinger collection, and also in the ZSMC. Despite inspecting every *Damas* specimen among the entire Hesperiidae holdings, N.V.G. failed to find a specimen from Panama collected by Ribbe and agreeing with the original description of *H. angulis*. Therefore, we believe that syntypes of this taxon were lost. Not finding syntypes, we proceeded with the neotype designation because there is an exceptional need to clarify the taxonomic identity of *H. angulis* and define it objectively due to new species present in the complex, multiple synonymic names, likely incorrect type localities for some taxa, and a non-syntypic specimen, possibly from Mexico or Guatemala, identified by Plötz as *H. angulis* that is not conspecific with specimens collected in Panama. To address all these problems, hereby, N.V.G. designates the specimen in USNM illustrated in Fig. 148b (DNA sample NVG-23122H05) as the **neotype** of *Hesperia angulis* Plötz, 1886.

This neotype satisfies all requirements set forth by the ICZN Article 75.3, namely: **75.3.1.** It is designated to clarify the taxonomic identity of *Hesperia angulis* Plötz, 1886, which is necessary because additional species are present among its close relatives; **75.3.2.** The characters to differentiate this taxon from others were given in the original description (Plötz 1886) that was translated above. We regard them as follows, adding male genitalic characters: an elongated hyaline spot along the lower side of the discal cell on the forewing, an angle-shaped hyaline spot in the forewing cell CuA_1-CuA_2, a square hyaline spot near the base of forewing cell M_3-CuA_1, a dot-shaped hyaline spot in the forewing cell R_5-M_1, a diffuse spot of pale scales near the middle of the forewing cell CuA_2-1A+2A near the 1A+2A vein, this spot is much more prominent on the ventral side, otherwise mostly dark brown; the posteriorly directed spike-like process of the tegumen is not reaching the end of the uncus, the harpe is terminally rounded, with a longer dorsoposterior margin that is finely serrated and with a narrower tooth by the ampulla that is directed anterodorsad, uncus arms are slightly divergent, shorter than in the closest relatives; **75.3.3.** The neotype specimen is a male bearing two rectangular white labels (1st handwritten, 2nd printed): [Bayano | Pma. Panama | 26 05 74 | G B Small], [DNA sample ID: | NVG-23122H05 | c/o Nick V. Grishin], and illustrated in Fig. 148b; the neotype is a specimen in excellent condition, has its head tilted to the right, proboscis expanded anteriad, and some scales rubbed off at the bases of both forewings and near the right forewing apex above; **75.3.4.** As detailed above, we carefully searched for syntypes of *H. angulis* in the MFNB and other collections. We failed to find the syntypes among Hesperiidae holdings in these collections and, therefore, believe that they were lost; **75.3.5.** The neotype closely agrees with the original description of *H. angulis* in all characters, as evidenced by comparing the neotype illustrated in Fig. 148b with the characters for this taxon given in the original description (Plötz 1886) and listed above (75.3.2.); **75.3.6.** The neotype is from Panama: Panama, and the original type locality was in Panama, which may be narrowed down to central Panama, in contrast to Chiriquí, as usually stated in the labels of specimens collected by Ribbe, who collected the type series; **75.3.7.** The neotype is in the National Museum of Natural History, Washington, DC, USA (USNM). The COI barcode sequence of *H. angulis* neotype, sample NVG-23122H05, GenBank PV550069, 658 base pairs, is:

AACTTTATATTTTATTTTTGGTGTATGAGCAGGATTATTAGGAACTTCCTTAAGTATACTAATTCGAACAGAATTAGGAAATCCTGGATCTTTAATTGGAGACGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAACTGATTAGTACCTTTAATATTAGGTGCTCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGGATACTACCCCCATCCTTAATCTTATTAATTTCAAGAAGAATCGTAGAAACTGGAGCAGGAACTGGTTGAACTGTTTACCCCCCCCTTTCATCCAATATTGC
CCACCAAGGAGCTTCAGTAGATTTAGCTATTTTTTCTCTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATCAATTTTATTACCACAATTATTAATATACGAGTAAAAAATTTATCC
TTTGATCAAATACCATTATTTATTTGATCCGTAGGAATTACAGCTCTCTTATTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAACCTTAATACTT
CTTTTTTTGATCCAGCTGGCGGAGGAGATCCTATTTTATATCAACATTTATTT

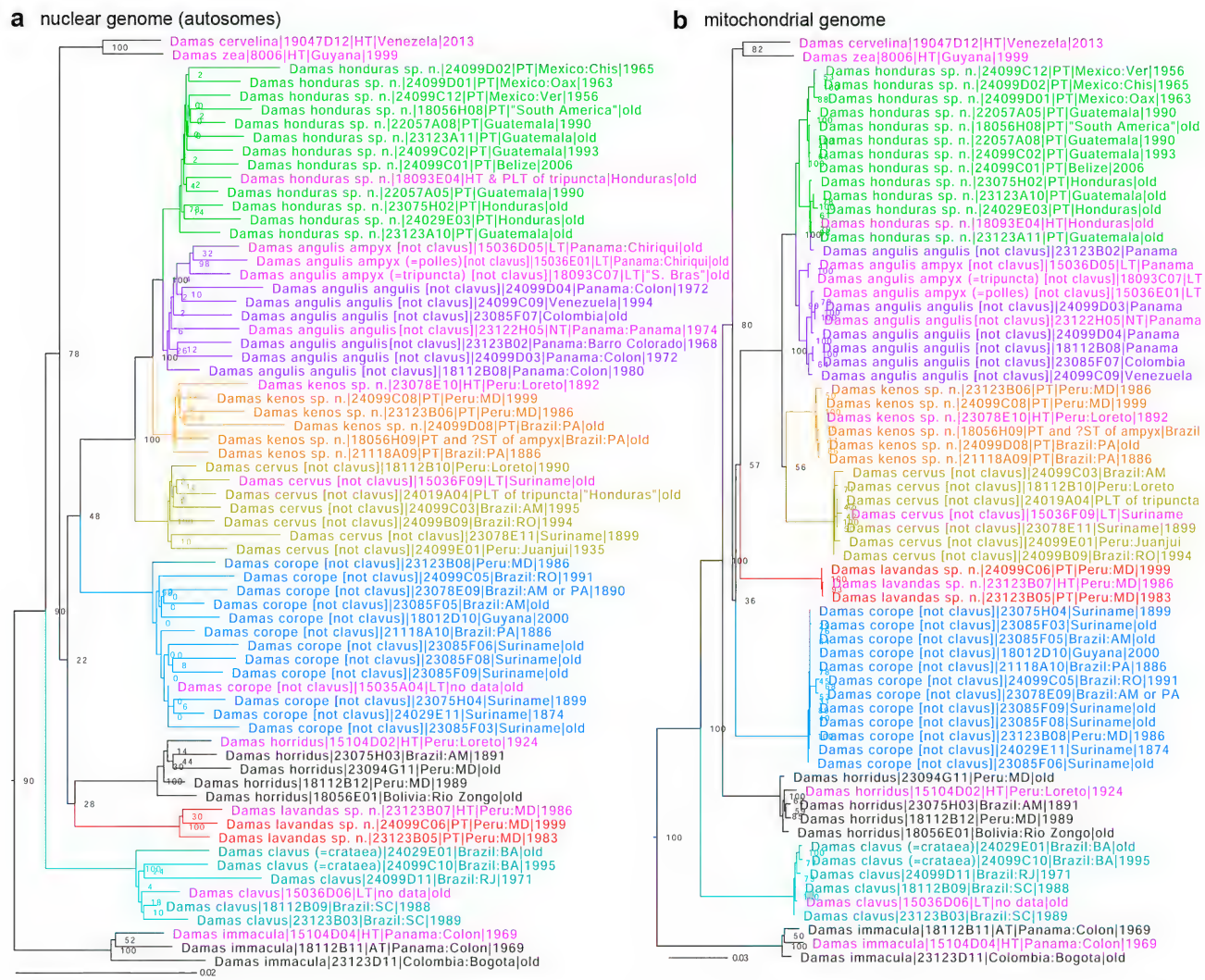


Fig. 152. Phylogenetic trees of *Damas* inferred from protein-coding regions in: **a)** the nuclear genome (autosomes), **b)** the mitochondrial genome. Different taxa are shown in different colors: *D. honduras* **sp. n.** (green), *D. angulis* **stat. rest.** (purple), *D. kenos* **sp. n.** (orange), *D. cervus* **stat. rest.** (olive), *D. corope* **stat. rest.** (blue), *D. lavandas* **sp. n.** (red), and *D. clavus* (cyan). Primary type specimens are labeled in magenta.

Species delimitation and synonymy in the *Damas clavus* (Herrich-Schäffer, 1869) complex

Having achieved an objective definition of all names in the *Damas clavus* (Herrich-Schäffer, 1869) complex and a better understanding of their type localities, we now proceed with the species delimitation. Genomic analysis of sequenced specimens that included primary types of nearly all available names (except *Hesperia crataea* Hewitson, 1876 (type locality in Brazil: Bahia) and *Damas woldi* Shuey, 2024 (type locality in French Guiana)) reveals that the complex consists of several species (Fig. 152). *Damas clavus* (Herrich-Schäffer, 1869) (type locality in Southeast or South Brazil, lectotype sequenced as NVG-15036D06) is most distantly related to others (Fig. 152 cyan). Sequenced specimens from Bahia, Brazil, where the lectotype of *Hesperia crataea* Hewitson, 1876 was collected, are placed within this species. Therefore, we maintain the synonymy of *Hesperia crataea* Hewitson, 1876 with *D. clavus*. However, all other taxa currently regarded as synonyms of *D. clavus* are either distinct species or synonyms of each other. Guided by the name priority, *Goniloba corope* Herrich-Schäffer, 1869 (type locality in the Amazonian region, lectotype sequenced as NVG-15035A04), *Proteides cervus* Möschler, 1877 (type locality in Suriname, lectotype sequenced as NVG-15036F09), and *Hesperia angulis* Plötz, 1886 (type

locality in Panama: Panama, neotype sequenced as NVG-23122H05) are genetically differentiated from *D. clavus* and each other at the species level (Fig. 152), e.g., COI barcodes of the closest species pair *P. cervus* and *H. angulis* differ by 3.5% (23 bp). Therefore, we propose that *Damas corope* (Herrich-Schäffer, 1869), **stat. rest.**, *Damas cervus* (Möschler, 1877), **stat. rest.**, and *Damas angulis* (Plötz, 1886), **stat. rest.** are species-level taxa distinct from *Damas clavus* (Herrich-Schäffer, 1869).

We find that the lectotype of *D. corope* belongs to a clade with a wide range in the Amazonian region from Guyana and Suriname to Rondônia in Brazil and Madre de Dios in Peru (Fig. 152 blue). To show identification of *D. corope* and differences between species, we illustrate segments of the mitochondrial genome alignment of several *Damas* taxa, including their lectotypes (Fig. 153, the lectotype of *D. corope* is labeled in red font). Although we have not yet sequenced the holotype of *Damas woldi* and specimens from French Guiana, we hypothesize that they may belong to this clade due to phenotypic similarity and distribution. Therefore, we tentatively regard *Damas woldi* Shuey, 2024, **syn. nov.** as a junior subjective synonym of *Damas corope* (Herrich-Schäffer, 1869), **stat. rest**.

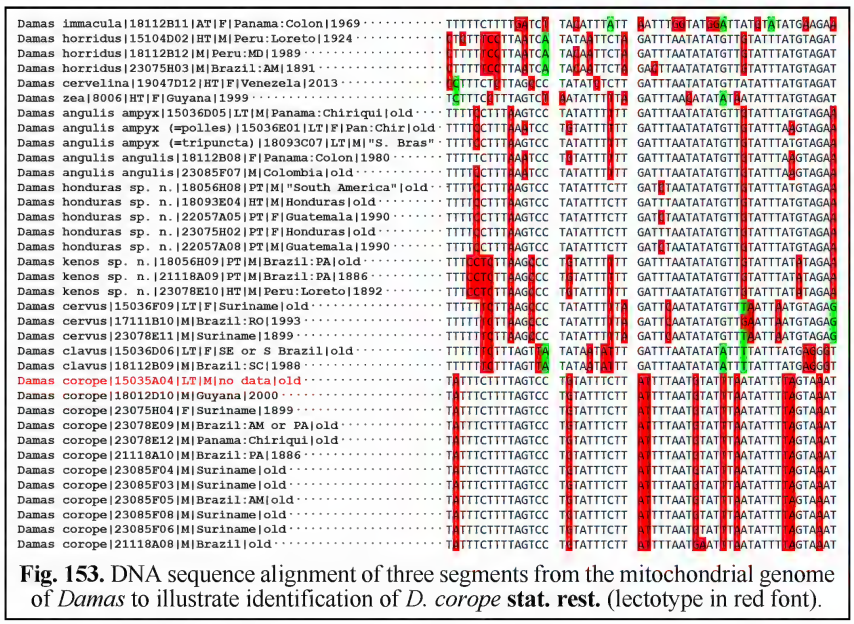


Fig. 153. DNA sequence alignment of three segments from the mitochondrial genome of *Damas* to illustrate identification of *D. corope* **stat. rest.** (lectotype in red font).

Specimens from Chiriquí, Panama, form a tight subclade within *D. angulis* in the nuclear genome tree and are genetically differentiated from others to warrant at least a subspecies status (Fig. 152 purple clade); e.g., their COI barcodes differ by 1.5% (10 bp). Therefore, we propose that *Proteides ampyx* Mabille, 1891 (type locality in Panama: Chiriquí, lectotype sequenced as NVG-15036D05) is a subspecies of *Damas angulis* (Plötz, 1886), **stat. rest.**: *Damas angulis ampyx* (Mabille, 1891), **stat. nov**. The lectotype of *Thracides polles* Godman, 1901 (type locality in Panama: Chiriquí, sequenced as NVG-15036E01) and, to our surprise, the lectotype of *Perichares tripuncta* Draudt, 1923 (type locality stated as South Brazil on the label, sequenced as NVG-18093C07) group closely with the lectotype of *D. angulis ampyx*, and therefore, we regard the two former taxa as junior subjective synonyms of the latter, a **new** placement of synonyms. This result implies that the lectotype of *P. tripuncta* has been mislabeled and was most likely collected in Chiriquí, Panama. Note the angle-shaped hyaline spot in the forewing cell CuA_1-CuA_2 and a long discal cell hyaline dash characteristic of Panamanian specimens in the lectotype of *P. tripuncta*: images of this specimen photographed by E. Brockmann are shown on the Butterflies of America website (Warren et al. 2024). Furthermore, we find three species-level clades that do not have available names associated with them and, therefore, represent new species, which are described next.

Damas honduras Grishin, new species

http://zoobank.org/3E984A36-0510-48F1-BEE1-4FB2E09D34F4

(Figs. 148c, 149h–i, 152 part, 153 part)

Definition and diagnosis. Specimens from the northern part of the range of the *Damas clavus* (Herrich-Schäffer, 1869) (type locality in Southeast or South Brazil) complex form a clade sister to *Damas angulis* (Plötz, 1886) **stat. rest.** (type locality in Panama: Panama) genetically differentiated from it at the species level (Fig. 152 green vs. purple); e.g., their COI barcodes differ by 2.0% (13 bp), and, therefore, represent a new species. This new species keys to *Damas clavus* (K.26) in Evans (1955) and differs from all its

congeners by the combination of the following characters in males: a larger elongated hyaline spot along the lower side of the discal cell on the forewing, a crescent-shaped (broader than in a typical *D. angulis*) hyaline spot in the forewing cell CuA_1-CuA_2, a rectangular (longer than a typical square-shaped spot of *D. angulis*) hyaline spot near the base of forewing cell M_3-CuA_1, a dot-shaped hyaline spot in forewing cell R_5-M_1, a diffuse spot of pale scales near the middle of forewing cell CuA_2-1A+2A near the 1A+2A vein, this spot is much more prominent on the ventral side, otherwise mostly dark brown; the lower portion of the stigma is nearly square, stronger offset distad from the upper portion, which is elongated rather than triangular; the posteriad-directed process of the tegumen is narrower, the uncus is deeper divided, the harpe is more robust with a broader tooth at the base of its dorsal margin. Due to the cryptic nature of this species and poorly explored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly1838.42.1:G96A, aly1838.42.1:G123A, aly85.33.2:C349T, aly85.33.2:A606G, aly706.2.3:G102A. This species may not differ from *D. angulis* in the COI barcode, possibly due to introgression (e.g., specimen NVG-23123B02 in Fig. 152b).

Barcode sequence of the holotype. Sample NVG-18093E04, GenBank PV550070, 658 base pairs:

AACTTTATATTTTATTTTCGGTGTCTGAGCAGGATTACTAGGAACTTCCTTAAGTATACTAATTCGAACAGAATTAGGAAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTGCCTTTAATATTAGGTGCCCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGGATACTACCCCCATCCTTAATCTTATTAATTTCAAGAAGAATCGTAGAAACTGGAGCAGGAACTGGTTGAACTGTCTACCCCCCCCTTTCATCCAATATTGC
TCACCAAGGAGCTTCAGTAGATTTAGCTATTTTTTTCTCTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATCAATTTTATTACCACAATTATTAATATACGAGTAAGAAATTTATCC
TTTGATCAAATACCATTATTTATTTGATCCGTAGGAATTACAGCTCTTTTATTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATACTACTTACTGATCGAAACCTTAATACTT
CTTTTTTTGATCCAGCTGGTGGAGGAGATCCTATTTTATATCAACATTTATTT

Type material. Holotype: ♂ deposited in the Senckenberg Natural History Museum, Frankfurt, Germany (SMF), illustrated in Fig. 148c, bears the following five printed (text in italics handwritten) rectangular labels (1st grayish-green, 2nd and last red, others white): [Honduras | San Pedro Sula | ex coll. Fruhstorfer], [Para*lec-* | *to*typus], [Paralectotypus | *Perichares* | *tripuncta* | *Draudt, 1923* | O Mielke det 19*79*], [DNA sample ID: | NVG-18093E04 | c/o Nick V. Grishin], and [HOLOTYPE ♂ | Damas honduras | Grishin]. The holotype is also a paralectotype of *Perichares tripuncta* Draudt, 1923 (type locality in Panama: Chiriquí as deduced by the genomic sequencing of the lectotype NVG-18093C07, not S. Brazil). Images of this specimen photographed by E. Brockmann are shown on the Butterflies of America website (Warren et al. 2024). **Paratypes:** 9♂♂ and 4♀♀: Mexico, T. Escalante leg. [MGCL]: 1♂ NVG-24099D02 Chiapas, Santa Rosa Comitán, Sep-1965; 2♂♂ Oaxaca, Chimalapa: NVG-24099D01 Sep-1963 and NVG-24099C11 Sep-1965; and 1♂ NVG-24099C12 Veracruz, Catemaco, Sep-1956; Guatemala: Petén, Tikal: 1♂ NVG-22057A08 and 1♀ NVG-22057A05 7-Jan-1990, C. J. Durden leg. [TMMC] and 1♂ NVG-24099C02, UF FLMNH MGCL 104891 11-Sep-1993, D. L. Lindsley leg. [MGCL] and Cayuga, old, Schaus & Barns collection [USNM]: 1♂ NVG-23123A10, genitalia NVG240817-69 (Fig. 149h, i) and 1♀ NVG-23123A11; 1♀ NVG-24099C01 Belize, Orange Walk District, Gallon Jug, Jan-2006, J. Benner collection [MGCL]; Honduras San Pedro Sula, old [MFNB]: 1♂ NVG-24029E03 Coll. Thieme and 1♀ NVG-23075H02; and 1♂ NVG-18056H08 "South America" [likely Guatemala], old [ZSMC].

Type locality. Honduras: San Pedro Sula.

Etymology. The name rhymes with the genus name and is given for the country with the type locality. The name is treated as a noun in apposition.

Distribution. From southern Mexico to Honduras.

Comment. Note that the genitalia of *Damas* are sclerotized more weakly than most other Hesperiidae and thus appear paler (Fig. 149).

Damas kenos Grishin, new species

http://zoobank.org/F274D8A9-4E44-4704-84BF-C1AAF9939812

(Figs. 148d, 149j–k, 152 part, 153 part)

Definition and diagnosis. Several specimens from the Amazonian region are genetically differentiated from other *Damas* Godman, 1901 (type species *Goniloba clavus* Herrich-Schäffer, 1869) at the species level, forming a separate clade sister to several other species in the genus (Fig. 152 orange) and, therefore, represent a new species. This new species keys to *Damas clavus* (K.26) in Evans (1955) but differs from

all its congeners by the combination of the following characters in males: the lack (or a trace) of the discal cell spot on the forewing, narrower brand (with the 3rd small dot-shaped segment in the middle of the cell CuA_2-1A+2A, only slightly longer (along the CuA_2 vein) than wide brand segment below the CuA_2 vein, nearly triangular semi-hyaline spot in cell CuA_1-CuA_2 with only slightly concave outer margin; dark ventral hindwing with little purple gloss, only slightly paler area towards the inner margin of dorsal forewing with a diffuse cream spot (smaller than the spot in the cell CuA_1-CuA_2) in the middle of the cell CuA_2-1A+2A, more extensive on the underside; one small subapical spot; head brownish-gray, including ventral side of the palpi and cheeks. Due to the somewhat cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly318.43.4:A87G, aly318.43.4:T117C, aly686.10.2:T42G, aly686.10.2:A63G, aly4740.1.1:C969T; and COI barcode: A79G, T82C, T106C, A331G, T428C.

Barcode sequence of the holotype. Sample NVG-23078E10, GenBank PV550071, 658 base pairs:

AACTTTATATTTTATTTTTGGTGTATGAGCAGGATTATTAGGAACTTCCTTAAGTATACTAATTCGAACAGAATTAGGGAACCCTGGATCTTTAATTGGAGATGACCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCTTTAATATTAGGTGCTCCTGATATAGCTTTCCCTCGAA
TAAATAATATAAGATTTTGGATACTACCCCCATCCTTAATCTTATTAATTTCAAGAAGAATCGTAGAAACTGGAGCAGGAACTGGTTGGACTGTTTACCCCCCTCTTTCCTCCAATATTGC
CCACCAAGGAGCTTCAGTAGATTTAGCTATTTTTTCTCTACATTTAGCAGGAATTTCTTCTATTCTAGGAGCAATCAATTTTATTACTACAATCATTAATATACGAGTAAGAAACTTATCC
TTTGATCAAATACCATTATTTATTTGATCAGTAGGAATTACAGCTCTTTTATTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAACCTTAATACTT
CTTTTTTTGATCCAGCTGGTGGAGGAGATCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the Museum für Naturkunde, Berlin, Germany (MFNB), illustrated in Fig. 148d, bears the following four printed rectangular labels, three white: [Iquitos | Amazon. Sup. | 1892. Michael], [Coll. Staudinger], [DNA sample ID: | NVG-23078E10 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Damas kenos | Grishin]. The holotype was collected in 1892 by Otto Michael. **Paratypes:** 4♂♂ and 1♀: Peru, Madre de Dios, Tambopata Reserve: 1♂ NVG-23123B06 Rio la Torre, 1-Oct-1986. S. S. Nicolay leg., genitalia NVG240817-70 (Fig. 149j, k) [USNM] and 1♀ NVG-24099C08 60 km S of Puerto Maldonado, Rio Tambopata, 25-Oct-1999, D. & J. Lindsley leg. [MGCL] and Brazil, Pará: 1♂ NVG-24099D08 Santarem, ex coll. Le Moult; 1♂ NVG-21118A09 1886, Donckier leg. [MFNB] and 1♂ NVG-18056H09 "Amaz. Inf." P. Hahnel leg. [ZSMC]. The last specimen is labeled as a "paratype" of *Proteides ampyx* Mabille, 1891 (type locality in Panama: Chiriquí). However, it is not from the type locality and, therefore, is not a syntype of that taxon.

Type locality. Peru: Loreto Region, Iquitos.

Etymology. In Greek, κενός (kenos) means empty or void and is given for the lack of a pale spot in the discal cell of the forewing in this species. The name is treated as an indeclinable adjective.

Distribution. The Amazonian region from north-eastern Peru to the lower Amazon.

Damas lavandas Grishin, new species

http://zoobank.org/008D4653-DE83-4E6D-B40A-050D3C1C8F2A

(Figs. 149l–m, 152 part, 154)

Definition and diagnosis. Three specimens from the Tambopata National Reserve are genetically differentiated from other *Damas* Godman, 1901 (type species *Goniloba clavus* Herrich-Schäffer, 1869) at the species level, forming a separate clade in the deep radiation of the genus (Fig. 152 red) and, therefore, represent a new species. This new species keys to *Damas clavus* (K.26) in Evans (1955) and differs from all its congeners by the combination of the following characters in males: strong purple tinge on the ventral side of wings: in the apical third of the forewing and most of the hindwing except the posterior third; smaller stigma with a shorter and rounder upper section; three subapical semi-hyaline spots; forewing discal cell with a single semi-hyaline yellowish smaller spot at the lower part of the forewing discal cell; the posteriorly directed spike-like process of the tegumen is not reaching the end of the uncus, the harpe is terminally rounded, with a longer and slightly concave dorsoposterior margin that is finely serrated and with a narrower tooth by the ampulla that is directed anterodorsad, uncus arms are terminally converging, narrower. Due to the partly cryptic nature of this species and unexplored individual variation, most reliable identification is achieved by DNA, and a combination of the following base pairs is diagnostic in the nuclear genome: aly390.22.4:A72G, aly390.22.4:G105A, aly822.25.2:A105G, aly26.20.2:G531A, aly26.20.2:G552A; and COI barcode: T151C, T178C, T205C, C277T, T523C.

Fig. 154. *Damas lavandas* **sp. n.** holotype ♂ NVG-23123B07 in dorsal (left) and ventral (right) views, data in text, at the same scale as Fig. 148. The inset displays a magnified view (scale indicated by 0.5 cm bar) of the middle of the forewing, highlighting digitally enhanced stigma.

Barcode sequence of the holotype. Sample NVG-23123B07, GenBank PV550072, 658 base pairs:

AACTTTATATTTTATTTTTGGTATTTGAGCAGGATTACTAGGAACTTCTTTAAGTATATTAATTCGAACAGAATTAGGAAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATACA
ATTGTTACAGCTCATGCCTTTATTATAATCTTTTTTATAGTTATACCTATTATAATCGGAGGATTTGGTAATTGATTAGTACCCTTAATATTAGGTGCCCCTGATATAGCTTTCCCCCGAA
TAAATAATATAAGATTTTGAATATTACCTCCATCTTTAATCTTATTAATTTCAAGAAGAATCGTAGAAACTGGAGCAGGAACTGGTTGAACTGTTTACCCCCCTCTTTCCTCCAATATTGC
TCACCAAGGAGCTTCAGTAGATTTAGCTATTTTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCAATTAATTTTATTACTACAATCATTAATATACGTGTAAGAAATTTATCA
TTTGATCAAATACCCTTATTTGTATGATCAGTAGGAATCACAGCCCTTTTACTACTTTTATCTTTACCAGTTTTAGCAGGAGCTATTACTATATTACTTACTGATCGAAATCTTAATACTT
CTTTTTTTGATCCAGCTGGAGGAGGAGATCCTATTTTATACCAACATTTATTT

Type material. Holotype: ♂ deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), illustrated in Fig. 154, bears the following three printed (text in italics handwritten) rectangular labels, two white: [PERU Madre De Dios | Rio La Torre 300m | Tambopata Res. | *29 Sept.'86* | S. S. Nicolay], [DNA sample ID: | NVG-23123B07 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Damas lavandas | Grishin]. **Paratypes:** 2♂♂ from Peru, Madre de Dios: 1♂ NVG-23123B05 30 km SW of Puerto Maldonado, 300 m, 17-Oct-1983, S. S. Nicolay leg. [USNM] and 1♂ NVG-24099C06 (leg DNA extraction, sequenced), NVG-24127F09 (abdomen DNA extraction and dissection) 60 km S of Puerto Maldonado, Rio Tambopata, 25-Oct-1999, D. & J. Lindsley leg., genitalia NVG250517-06 (Fig. 149l, m) [MGCL].

Type locality. Peru: Madre de Dios Region, Tambopata National Reserve, Rio La Torre, elevation 300 m.

Etymology. In Spanish, lavanda means lavender. The name rhymes with the genus name and is given for the purplish sheen on the ventral side of this species. The name is treated as a noun in apposition.

Distribution. Currently known only from the Tambopata National Reserve in southeastern Peru.

Comment. This species is sympatric with *Damas kenos* **sp. n.**, in the Tambopata National Reserve, Peru.

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